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Transitional Vertebrate Fossils FAQ

[Last Update: March 17, 1997]

I wrote this FAQ as a reference for answering the "there aren't any transitional fossils" statement that pops up on talk.origins several times each year. I've tried to make it an accurate, though highly condensed, summary of known vertebrate fossil history in those lineages that led to familiar modern forms, with the known transitions *and* with the known major gaps both clearly mentioned. Version 6.0 of the FAQ has been almost entirely rewritten, with:

1. A completely rewritten introduction & conclusion, discussing what "transitional" means, why gaps occur, and what the fossil record shows.
2. A greatly expanded list of "chains of genera" for most groups, especially mammals.
3. References for documented species-to-species fossil transitions, mostly for mammals.
4. Explicit mention of the notable remaining gaps in the fossil record.

If you have questions about this FAQ or want to send email to the author, click here.

Contents

PART I has FISHES TO FIRST MAMMALS & BIRDS:

PART 2 has transitions among mammals (starting with primates), including numerous species-to-species transitions, discussion, and references. If you're particularly interested in humans, skip to the primate section of part 2, and also look up the fossil hominid FAQ.

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Transitional Vertebrate Fossils FAQ
Contacting the Author

Before contacting the author, please read the following common questions about the Transitional Fossils FAQ:

1. "The FAQ doesn't have *real* transitional fossils"

> If you have just skimmed part of the FAQ and concluded that it doesn't have what you consider to be "real" transitional fossils, go back to part 1 of the FAQ and carefully read the section titled "What is a transitional fossil?" Think about what you have read. Then read the rest of the FAQ, and pay particular attention to the "species-to-species" sections in part 2. If you still think the FAQ doesn't have "real" transitional fossils, chances are you have misunderstood the theory of evolution. Define what a "real" transitional fossil should be, and why you think the modern theory of evolution would predict such a thing. Then let's talk.

2. "Yeah, okay, but if the dating techniques are wrong, doesn't that make the whole 'fossil record' fall apart?"

> This is a good question, but it is outside the scope of this FAQ (which is long enough as it is). The short answer is yes, the fossil record depends utterly on accurate dating techniques. Dating techniques come in two basic (and independent) varieties: *relative* techniques, which tell you whether a fossil layer is older or younger than another layer, and *absolute* techniques, which give a numerical age for a rock. Describing these techniques in detail would require a whole nother set of FAQs. (See, for example, the FAQ on radiometric dating). In a nutshell, though, if the techniques are applied carefully they are surprisingly accurate, and independent methods show a remarkable tendency to come up with the same date. If you want to learn more about this field, get a copy of Prothero's "Sedimentary Geology" or another geology text and read it *thoroughly*.

3. "I don't have time to read the whole FAQ, so could you just answer the following question for me?" (followed by a complicated two-page series of questions, some of which have nothing to do with fossils)

> People who send me this sort of e-mail may expect a short-tempered response! If you didn't have time to read the FAQ - or any of the other talk.origins FAQs - why should I have the time to write a detailed response to spoon-feed the information to you? It took a *lot* of time to write this FAQ, and it also takes a *lot* of time to write long e-mail responses. I love teaching biology, and it would be great if I had a full-time job to teach biology by e-mail; but unfortunately, I have to do it in my spare time, which I do not have a lot of.
>
> Face it, learning about biology takes time, and you are just going to have to buckle down and read the FAQs -- yes, the whole darned fossil FAQ and the whole darned other t.o. FAQs as well.

4. "Why isn't the FAQ illustrated?"

> The primary reasons are practical: there aren't any un-copyrighted illustrations available, and I don't own a scanner (or even a modem, or even [gasp] a web surfer). Furthermore, creating good fossil illustrations would be extremely difficult, for the following reasons. Many of the fossil illustrations seen in textbooks are actually very inaccurate (for instance, Hyracotherium is usually drawn to look like a little horse; but in fact, it did not look at all like a horse). Good fossil illustrations can only be done by a small subset of scientific illustrators who are trained in anatomy and paleontology. Hiring one of these people would cost actual money. The illustrator would then have to spend several years flying to 50 or so museums to see the original fossils and talking to the expert paleontologists who have studied each fossil. Furthermore, the species-to-species transitions would be tricky to illustrate, since they involve whole populations of hundreds

of fossils simultaneously showing gradual shifts in various traits. It would be an exciting project -- but doing it right would take years and would require substantial funding for salaries, travel, and equipment.

5. **"Why hasn't the transitional fossils FAQ been updated recently?"**

   Lack of time and money. The talk.origins FAQs are not organized by any central entity, and are not funded at all. They are just written by people who know the subject matter, got inspired, and felt like spending long hours of their (unpaid) time writing a FAQ. This FAQ is a typical example. I wrote the first version in 1991 (inspired by the astonishing ignorance exhibited on talk.origins). I updated it regularly until 1994. Each update took a significant amount of time (several months' part-time work, unpaid). This was possible because in those years I was a new grad student with a fully paid fellowship, no teaching duties, and no social life. I now have two part-time jobs, am finishing my PhD thesis, coordinating three other research projects, writing post-doc grants, and moving regularly to different houses (plus, I have a social life now). So unfortunately I no longer have time to update the FAQ. I plan someday, before I die, to fully update and publish a new fossils FAQ....but this may not happen till after the turn of the millenium! If you are knowledgable about vertebrate evolution and are interested in taking on the job, get in touch with me about doing the next FAQ update yourself.

6. **"What is the FAQ author's background?"**

   I'm a zoologist, currently working on my Ph.D. thesis in endocrinology and behavior at the Department of Zoology, University of Washington. I am not a paleontologist; rather, I am a vertebrate biologist who primarily studies living animals (not extinct ones). Most of my own research is on birds. I have a broad training in physiology, anatomy, behavior, and conservation biology, and I have taught or TA'd vertebrate anatomy, vertebrate natural history, vertebrate evolution, and general evolution. The history of vertebrate evolution is a pet side interest of mine. Writing this FAQ was a wonderful excuse to burrow into the primary literature and read a lot of fascinating textbooks and articles about vertebrate evolution.

Send your comments and suggestions to me, Kathleen Hunt, at: hunt@u.washington.edu. I welcome your feedback to the FAQ, but since I am often in the field, please be prepared to wait a while (usually weeks) for a email response. Thank you very much!

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Transitional Vertebrate Fossils FAQ
Part 1A

[Last Update: March 17, 1997]

Contents Part 1B

PART 1

1. Introduction

What is a transitional fossil?

The term "transitional fossil" is used at least two different ways on talk.origins, often leading to muddled and stalemated arguments. I call these two meanings the "general lineage" and the "species-to-species transition":

"General lineage":

> This is a *sequence of similar genera or families*, linking an older group to a very different younger group. Each step in the sequence consists of some fossils that represent a certain genus or family, and the whole sequence often covers a span of tens of millions of years. A lineage like this shows obvious morphological intermediates for every major structural change, and the fossils occur roughly (but often not exactly) in the expected order. Usually there are still gaps between each of the groups -- few or none of the speciation events are preserved. Sometimes the individual specimens are not thought to be *directly* ancestral to the next-youngest fossils (i.e., they may be "cousins" or "uncles" rather than "parents"). However, they are assumed to be closely related to the actual ancestor, since they have intermediate morphology compared to the next-oldest and next-youngest "links". The major point of these general lineages is that animals with intermediate morphology existed at the appropriate times, and thus that the transitions from the proposed ancestors are fully plausible. General lineages are known for almost all modern groups of vertebrates, and make up the bulk of this FAQ.

"Species-to-species transition":

> This is a set of *numerous individual fossils that show a change between one species and another*. It's a very fine-grained sequence documenting the actual speciation event, usually covering less than a million years. These species-to-species transitions are unmistakable when they are found. Throughout successive strata you see the population averages of teeth, feet, vertebrae, etc., changing from what is typical of the first species to what is typical of the next species. Sometimes, these sequences occur only in a limited geographic area (the place where the speciation actually occurred), with analyses from any other area showing an apparently "sudden" change. Other times, though, the transition can be seen over a very wide geological area. Many "species-to-species transitions" are known, mostly for marine invertebrates and recent mammals (both those groups tend to have good fossil records), though they are not as abundant as the general lineages (see below for why this is so). Part 2 lists numerous species-to-species transitions from the mammals.

Transitions to New Higher Taxa

> As you'll see throughout this FAQ, both types of transitions often result in a new "higher taxon" (a new genus, family, order, etc.) from a species belonging to a different, older taxon. There is nothing magical about this. The first members of the new group are not bizarre, chimeric animals; they are simply a new, slightly different species, barely different from the parent species. Eventually they give rise to a more different species, which in turn gives rise to a still more different species, and so on, until the descendents are radically different from the original parent stock. For example, the Order Perissodactyla (horses, etc.) and the Order Cetacea (whales) can both be traced back to early Eocene animals that looked only marginally different from each other, and didn't look *at all* like horses or whales. (They looked rather like small, dumb foxes with raccoon-like feet and simple teeth.) But over the following tens of millions of years, the descendents of those animals became more and more different, and now we call them two different orders.

There are now several known cases of species-to-species transitions that resulted in the first members of new higher taxa. See part 2 for details.

Why do gaps exist? (or seem to exist)

Ideally, of course, we would like to know each lineage right down to the species level, *and* have detailed species-to-species transitions linking every species in the lineage. But in practice, we get an uneven mix of the two, with only a few species-to-species transitions, and occasionally long time breaks in the lineage. Many laypeople even have the (incorrect) impression that the situation is even worse, and that there are no known transitions at all. Why are there still gaps? And why do many people think that there are even more gaps than there really are?

Stratigraphic gaps

> The first and most major reason for gaps is "stratigraphic discontinuities", meaning that fossil-bearing strata are not *at all* continuous. There are often large time breaks from one stratum to the next, and there are even some times for which no fossil strata have been found. For instance, the Aalenian (mid-Jurassic) has shown no known tetrapod fossils anywhere in the world, and other stratigraphic stages in the Carboniferous, Jurassic, and Cretaceous have produced only a few mangled tetrapods. Most other strata have produced at least one fossil from between 50% and 100% of the vertebrate families that we know had already arisen by then (Benton, 1989) -- so the vertebrate record at the family level is only about 75% complete, and *much* less complete at the genus or species level. (One study estimated that we may have fossils from as little as 3% of the species that existed in the Eocene!) This, obviously, is the major reason for a break in a general lineage. To further complicate the picture, certain types of animals tend not to get fossilized -- terrestrial animals, small animals, fragile animals, and forest-dwellers are worst. And finally, fossils from very early times just don't survive the passage of eons very well, what with all the folding, crushing, and melting that goes on. Due to these facts of life and death, there will always be some major breaks in the fossil record.
>
> Species-to-species transitions are even harder to document. To demonstrate *anything* about how a species arose, whether it arose gradually or suddenly, you need exceptionally complete strata, with many dead animals buried under constant, rapid sedimentation. This is rare for terrestrial animals. Even the famous Clark's Fork (Wyoming) site, known for its fine Eocene mammal transitions, only has about one fossil per lineage about every 27,000 years. Luckily, this is enough to record most episodes of evolutionary change (provided that they occurred at Clark's Fork Basin and not somewhere else), though it misses the rapidest evolutionary bursts. In general, in order to document transitions between species, you specimens separated by only tens of thousands of years (e.g. every 20,000-80,000 years). If you have only one specimen for hundreds of thousands of years (e.g. every 500,000 years), you can usually determine the order of species, but not the transitions between species. If you have a specimen every million years, you can get the order of genera, but not which species were involved. And so on. These are rough estimates (from Gingerich, 1976, 1980) but should give an idea of the completeness required.
>
> Note that fossils separated by more than about a hundred thousand years *cannot* show anything about how a species arose. Think about it: there could have been a smooth transition, or the species could have appeared suddenly, but either way, if there aren't enough fossils, we can't tell which way it happened.

Discovery of the fossils

> The second reason for gaps is that most fossils undoubtedly have not been found. Only two continents, Europe and North America, have been adequately surveyed for fossil-bearing strata. As the other continents are slowly surveyed, many formerly mysterious gaps are being filled (e.g., the long-missing

rodent/lagomorph ancestors were recently found in Asia). Of course, even in known strata, the fossils may not be uncovered unless a roadcut or quarry is built (this is how we got most of our North American Devonian fish fossils), and may not be collected unless some truly dedicated researcher spends a long, nasty chunk of time out in the sun, and an even longer time in the lab sorting and analyzing the fossils. Here's one description of the work involved in finding early mammal fossils: "To be a successful sorter demands a rare combination of attributes: acute observation allied with the anatomical knowledge to recognise the mammalian teeth, even if they are broken or abraded, has to be combined with the enthusiasm and intellectual drive to keep at the boring and soul-destroying task of examining tens of thousands of unwanted fish teeth to eventually pick out the rare mammalian tooth. On an average one mammalian tooth is found per 200 kg of bone-bed." (Kermack, 1984.)

Documenting a species-to-species transition is particularly grueling, as it requires collection and analysis of *hundreds* of specimens. Typically we must wait for some paleontologist to take it on the job of studying a certain taxon in a certain site in detail. Almost nobody did this sort of work before the mid-1970's, and even now only a small subset of researchers do it. For example, Phillip Gingerich was one of the first scientists to study species-species transitions, and it took him *ten years* to produce the first detailed studies of just two lineages (see part 2, primates and condylarths). In a (later) 1980 paper he said: "the detailed species level evolutionary patterns discussed here represent only six genera in an early Wasatchian fauna containing approximately 50 or more mammalian genera, *most of which remain to be analyzed*." [emphasis mine]

Getting the word out

There's a third, unexpected reason that transitions seem so little known. It's that even when they *are* found, they're not popularized. The only times a transitional fossil is noticed much is if it connects two noticably different groups (such as the "walking whale" fossil reported in 1993), or if illustrates something about the tempo and mode of evolution (such as Gingerich's work). Most transitional fossils are only mentioned in the primary literature, often buried in incredibly dense and tedious "skull & bones" papers utterly inaccessible to the general public. Later references to those papers usually collapse the known species-to-species sequences to the genus or family level. The two major college-level textbooks of vertebrate paleontology (Carroll 1988, and Colbert & Morales 1991) often don't even describe anything below the family level! And finally, many of the species-to-species transitions were described too recently to have made it into the books yet.

Why don't paleontologists bother to popularize the detailed lineages and species-to-species transitions? Because it is thought to be unnecessary detail. For instance, it takes an entire book to describe the horse fossils even partially (e.g. MacFadden's "Fossil Horses"), so most authors just collapse the horse sequence to a series of genera. Paleontologists clearly consider the occurrence of evolution to be a settled question, so obvious as to be beyond rational dispute, so, they think, why waste valuable textbook space on such tedious detail?

Misunderstanding of quotes about punctuated equilibrium

What paleontologists *do* get excited about are topics like the average rate of evolution. When exceptionally complete fossil sites *are* studied, usually a mix of patterns are seen: some species still seem to appear suddenly, while others clearly appear gradually. Once they arise, some species stay mostly the same, while others continue to change gradually. Paleontologists usually attribute these differences to a mix of slow evolution and rapid evolution (or "punctuated equilibrium": sudden bursts of evolution followed by stasis), in combination with the immigration of new species from the as-yet-undiscovered places where they first arose.

There's been a heated debate about which of these modes of evolution is most common, and this debate has been largely misquoted by laypeople, particularly creationists. Virtually all of the quotes of paleontologists saying things like "the gaps in the fossil record are real" are taken out of context from this ongoing debate about punctuated equilibrium. Actually, no paleontologist that I know of doubts that evolution has occurred, and most agree that *at least sometimes* it occurs gradually. The fossil evidence that contributed to that consensus is summarized in the rest of this FAQ. What they're arguing about is how *often* it occurs gradually. You can make up your own mind about that. (As a starting point, check out Gingerich, 1980, who found 24 gradual speciations and 14 sudden appearances in early Eocene mammals; MacFadden, 1985, who found 5 cases of gradual anagenesis, 5 cases of probable cladogenesis, and 6 sudden appearances in fossil horses; and the numerous papers in Chaline, 1983. Most studies that I've read find between 1/4-2/3 of the speciations occurring fairly gradually.)

Predictions of creationism and of evolution

Before launching into the transitional fossils, I'd like to run through the two of the major models of life's origins, biblical creationism and modern evolutionary theory, and see what they predict about the fossil record.

- Most forms of creationism hold that all "kinds" were created separately, as described in Genesis. Unfortunately there is no biological definition of "kind"; it appears to be a vague term referring to our psychological perception of types of organisms such as "dog", "tree", or "ant". In previous centuries, creationists equated "kind" to species. With the discovery of more and more evidence for derivation of one species from another, creationists bumped "kind" further up to mean higher taxonomic levels, such as "genus", or "family", though this lumps a large variety of animals in the same "kind". Some creationists say that "kind" cannot be defined in biological terms.

  Predictions of creationism: Creationists usually don't state the predictions of creationism, but I'll take a stab at it here. First, though there are several different sorts of creationism, all of them agree that there should be no transitional fossils at all between "kinds". For example, if "kind" means "species", creationism apparently predicts that there should be *no* species-to-species transitions whatsoever in the fossil record. If "kind" means "genus" or "family" or "order", there should be *no* species-to-species transitions that cross genus, family, or order lines. Furthermore, creationism apparently predicts that since life did not originate by descent from a common ancestor, fossils should not appear in a temporal progression, and it should not be possible to link modern taxa to much older, very different taxa through a "general lineage" of similar and progressively older fossils.

  Other predictions vary with the model of creationism. For instance, an older model of creationism states that fossils were created during six metaphorical "days" that may each have taken millenia to pass. This form of creationism predicts that fossils should be found in the same order outlined in Genesis: seed-bearing trees first, then all aquatic animals and flying animals, then all terrestrial animals, then humans.

  In contrast, many modern U.S. creationists believe the "Flood Theory" of the origin of fossils. The "Flood Theory" is derived from a strictly literal reading of the Bible, and states that all geological strata, and the fossils imbedded in them, were formed during the forty-day flood of Noah's time. Predictions of the Flood Theory apparently include the following:

    - most rock should be sedimentary and indicative of cataclysmic flooding. There should be no rock formations that indicate the passing of millenia of gradual accumulation of undisturbed sediment, such as multi-layered riverbed formations. There should be no large lava flows layered on top of each other, and definitely not with successively older radiometric dates in the lower levels.
    - terrestrial animal fossils should either not be sorted at all, or should be sorted by some "hydrodynamic" aspect such as body size, with, for instance, extinct elephants and large dinosaurs in the lowest layers, and small primitive dinosaurs in the upper layers. Terrestrial animal fossils should not be sorted by subtle anatomical details (such as, say, the number of cusps on the fourth premolar).
    - marine animals are a puzzle, since it is unclear that a Flood would cause any extinctions of aquatic animals. If such extinctions did occur, aquatic fossils would perhaps be "sorted" by body size or ecological niche (bottom-feeder vs. surface swimmer). For instance, plesiosaurs, primitive whales, and placoderm fishes (relatively slow-swimming and quite large) should end up in the same layers. Ichthyosaurs and porpoises (smaller, faster swimmers with almost identical body shapes and similar diets) should also occur in the same layers.
    - there should be no sorting of large rooted structures such as coral reefs and trees. There should likewise not be differential sorting of microscopic structures of the same size and shape, such as pollen grains.
    - sorting, if it occurs at all, should be quite imperfect. With only 40 days for sorting, there should be occasional examples of individual fossils that ended up in the "wrong" layer -- the occasional mammal and human fossil in Paleozoic rocks, for instance, and the occasional trilobite and plesiosaur in Cenozoic rocks.
    - sorting should *not* correlate with date of the surrounding rocks. If all fossils were created by Noah's flood, there is no conceivable reason that, for instance, lower layers of fossils should *always* end up sandwiched between lava rocks with old radiometric dates.

  Finally, some creationists believe that fossils were created by miraculous processes not operating today. (Many of these creationists combine this idea with the Flood Theory, as follows: fossils were created during the Flood, but were "sorted" by a miraculous process not observable or understandable today.) Obviously, such a theory makes no testable predictions...except perhaps for the prediction that geological formations should not bear any obvious resemblance to processes occurring today.

- Modern evolutionary theory holds that the living vertebrates arose from a common ancestor that lived hundreds of millions of years ago (via "descent with modification"; variety is introduced by mutation, genetic drift, and recombination, and is acted on by natural selection). Various proposed mechanisms of evolution differ in the expected rate and tempo of evolutionary change.

  Predictions of evolutionary theory: Evolutionary theory predicts that fossils *should* appear in a temporal progression, in a nested hierarchy of lineages, and that it *should* be possible to link modern animals to older, very different animals. In addition, the "punctuated equilibrium" model also predicts that new species should often appear "suddenly" (within 500,000 years or less) and then experience long periods of stasis. Where the record is exceptionally good, we should find a few local, rapid transitions between species. The "phyletic gradualism" model predicts that most species should change gradually throughout time, and that where the record is good, there should be many slow, smooth species-to-species transitions. These two models are not mutually exclusive -- in fact they are often viewed as two extremes of a continuum -- and both agree that at least *some* species-to-species transitions should be found.

What's in this FAQ

This FAQ mostly consists of a *partial* list of known transitions from the vertebrate fossil record. The transitions in part 1 are mostly general lineages, while in part 2 there are both general lineages and species- to-species transitions. In a hopeless attempt to save space, I concentrated almost exclusively on groups that left living descendants, ignoring all the hundreds of other groups and side-branches that have died out. I also skipped entire groups of vertebrates (most notably the dinosaurs and modern fish) in order to emphasize mammals, the group talk.origins'ers are most interested in. Note that the general lineages sometimes include "cousin" fossils. These are fossils that are thought to be very similar and closely related to the actual ancestor, but for various reasons are suspected *not* to be that ancestor. I have labelled them clearly in the text. I've also pointed out some of the significant remaining gaps in the vertebrate fossil record.

I got most of the information from Colbert & Morales' *Evolution of the Vertebrates* (1991), Carroll's *Vertebrate Paleontology and Evolution* (1988), Benton's *The Phylogeny and Classification of the Tetrapods* (1988), and from various recent papers from the scientific literature. These sources are all listed in the reference section at the end of part 2.

The time of first known appearance of each fossil is given in parentheses after the fossil name, including absolute dates when I could find them. The only exceptions are a few cases where my source didn't mention a date and it wasn't listed in Carroll's text. All of these fossils were dated by *independent* means, typically by using several different methods of radiometric dating on the strata around the fossil, and/or by cross-correlating to dated strata at other sites (e.g. MacFadden et al., 1991). **The information in this FAQ assumes that these dating methods are accurate**. If you have questions about the many dating methods used by paleontologists, see the other FAQs on those topics and get yourself a good textbook of sedimentary geology. Paleontologists are generally sharp cookies, and are quite persnickety about using good dating techniques.

Some terminology

"**Anagenesis**", "**phyletic evolution**":

Evolution in which an older species, as a whole, changes into a new descendent species, such that the ancestor is transformed into the descendant.

"**Cladogenesis**":

Evolution in which a daughter species splits off from a population of the older species, after which both the old and the young species coexist together. *Notice that this allows a descendant to coexist with its ancestor*.

"**Chronocline**":

Gradual change in one lineage over time

Ma:

Millions of years ago (a date)

my:

Millions of years (a duration)

Timescale

CENOZOIC		
(See part 2)	65-0 Ma	Mammals & birds & teleost fish dominant
MESOZOIC		
Cretaceous	144-65 Ma	Dinosaurs dominant. Small mammals, birds.
Jurassic	213-144 Ma	Dinosaurs dominant. First mammals, then first birds.
Triassic	248-213 Ma	Mammalian reptiles dominant. First dinosaurs.
PALEOZOIC		
Permian	286-248 Ma	Amphibians dominant. First mammal-like reptiles.
Pennsylvanian	320-286 Ma	Amphibians dominant. First reptiles.
Mississippian	360-320 Ma	Big terrestrial amphibians, fishes.
Devonian	408-360 Ma	Fish dominant. First amphibians.
Silurian	438-408 Ma	First ray-finned & lobe-finned fish.
Ordovician	505-438 Ma	More jawless fishes.
Cambrian	590-505 Ma	First jawless fishes.

Summary of the known vertebrate fossil record

(We start off with primitive jawless fish.)

Transition from primitive jawless fish to sharks, skates, and rays

- Late Silurian -- first little simple shark-like denticles.
- Early Devonian -- first recognizable shark teeth, clearly derived from scales.

GAP: Note that these first, very very old traces of shark-like animals are so fragmentary that we can't get much detailed information. So, we don't know which jawless fish was the actual ancestor of early sharks.

- *Cladoselache* (late Devonian) -- Magnificent early shark fossils, found in Cleveland roadcuts during the construction of the U.S. interstate highways. Probably *not* directly ancestral to sharks, but gives a remarkable picture of general early shark anatomy, down to the muscle fibers!
- *Tristychius* & similar hybodonts (early Mississippian) -- Primitive proto-sharks with broad-based but otherwise shark-like fins.
- *Ctenacanthus* & similar ctenacanthids (late Devonian) -- Primitive, slow sharks with broad-based shark-like fins & fin spines. Probably ancestral to all modern sharks, skates, and rays. Fragmentary fin spines (Triassic) -- from more advanced sharks.
- *Paleospinax* (early Jurassic) -- More advanced features such as detached upper jaw, but retains primitive ctenacanthid features such as two dorsal spines, primitive teeth, etc.
- *Spathobatis* (late Jurassic) -- First proto-ray.
- *Protospinax* (late Jurassic) -- A very early shark/skate. After this, first heterodonts, hexanchids, & nurse sharks appear (late Jurassic). Other shark groups date from the Cretaceous or Eocene. First true skates known from Upper Cretaceous.

A separate lineage leads from the ctenacanthids through *Echinochimaera* (late Mississippian) and *Similihari* (late Pennsylvanian) to the modern ratfish.

Transition from from primitive jawless fish to bony fish

- Upper Silurian -- first little scales found.

GAP: Once again, the first traces are so fragmentary that the actual ancestor can't be identified.

- Acanthodians(?) (Silurian) -- A puzzling group of spiny fish with similarities to early bony fish.
- Palaeoniscoids (e.g. *Cheirolepis*, *Mimia*; early Devonian) -- Primitive bony ray-finned fishes that gave rise to the vast majority of living fish. Heavy acanthodian-type scales, acanthodian-like skull, and big notochord.
- *Canobius*, *Aeduella* (Carboniferous) -- Later paleoniscoids with smaller, more advanced jaws.
- *Parasemionotus* (early Triassic) -- "Holostean" fish with modified cheeks but still many primitive features. Almost exactly intermediate between the late paleoniscoids & first teleosts. Note: most of these fish lived in seasonal rivers and had lungs. Repeat: lungs first evolved in *fish*.
- *Oreochima* & similar pholidophorids (late Triassic) -- The most primitive teleosts, with lighter scales (almost cycloid), partially ossified vertebrae, more advanced cheeks & jaws.
- *Leptolepis* & similar leptolepids (Jurassic) -- More advanced with fully ossified vertebrae & cycloid scales. The Jurassic leptolepids radiated into the modern teleosts (the massive, successful group of fishes that are almost totally dominant today). Lung transformed into swim bladder.

Eels & sardines date from the late Jurassic, salmonids from the Paleocene & Eocene, carp from the Cretaceous, and the great group of spiny teleosts from the Eocene. The first members of many of these families are known and are in the leptolepid family (note the inherent classification problem!).

Transition from primitive bony fish to amphibians

Few people realize that the fish-amphibian transition was *not* a transition from water to land. It was a transition from *fins to feet* that took place *in the water*. The very first amphibians seem to have developed legs and feet to scud around on the bottom in the water, as some modern fish do, not to walk on land (see Edwards, 1989). This aquatic-feet stage meant the fins didn't have to change very quickly, the weight-bearing limb musculature didn't have to be very well developed, and the axial musculature didn't have to change at all. Recently found fragmented fossils from the middle Upper Devonian, and new discoveries of late Upper Devonian feet (see below), support this idea of an "aquatic feet" stage. Eventually, of course, amphibians *did* move onto the land. This involved attaching the pelvis more firmly to the spine, and separating the shoulder from the skull. Lungs were not a problem, since lungs are an ancient fish trait and were present already.

- Paleoniscoids again (e.g. *Cheirolepis*) -- These ancient bony fish probably gave rise both to modern ray-finned fish (mentioned above), and also to the lobe-finned fish.
- *Osteolepis* (mid-Devonian) -- One of the earliest crossopterygian lobe-finned fishes, still sharing some characters with the lungfish (the other lobe-finned fishes). Had paired fins with a leg-like arrangement of major limb bones, capable of flexing at the "elbow", and had an early-amphibian-like skull and teeth.
- *Eusthenopteron*, *Sterropterygion* (mid-late Devonian) -- Early rhipidistian lobe-finned fish roughly intermediate between early crossopterygian fish and the earliest amphibians. *Eusthenopteron* is best known, from an unusually complete fossil first found in 1881. Skull very amphibian-like. Strong amphibian- like backbone. Fins very like early amphibian feet in the overall layout of the major bones, muscle attachments, and bone processes, with tetrapod-like tetrahedral humerus, and tetrapod-like elbow and knee joints. But there are no perceptible "toes", just a set of identical fin rays. Body & skull proportions rather fishlike.
- *Panderichthys*, *Elpistostege* (mid-late Devonian, about 370 Ma) -- These "panderichthyids" are *very* tetrapod-like lobe-finned fish. Unlike *Eusthenopteron*, these fish actually look like tetrapods in overall proportions (flattened bodies, dorsally placed orbits, frontal bones! in the skull, straight tails, etc.) and have remarkably foot-like fins.
- Fragmented limbs and teeth from the middle Late Devonian (about 370 Ma), possibly belonging to *Obruchevichthys* -- Discovered in 1991 in Scotland, these are the earliest known tetrapod remains. The humerus is mostly tetrapod-like but retains some fish features. The discoverer, Ahlberg (1991), said: "It [the humerus] is more tetrapod-like than any fish humerus, but lacks the characteristic early tetrapod 'L-shape'...this seems to be a primitive, fish-like character....although the tibia clearly belongs to a leg, the humerus differs enough from the early tetrapod pattern to make it uncertain whether the appendage carried digits or a fin. At first sight the combination of two such extremities in the same animal seems highly unlikely on functional grounds. If, however, tetrapod limbs evolved for aquatic rather than terrestrial

> locomotion, as recently suggested, such a morphology might be perfectly workable."

GAP: Ideally, of course, we want an *entire* skeleton from the middle Late Devonian, not just limb fragments. Nobody's found one yet.

- *Hynerpeton*, *Acanthostega*, and *Ichthyostega* (late Devonian) -- A little later, the fin-to-foot transition was almost complete, and we have a set of early tetrapod fossils that clearly did have feet. The most complete are *Ichthyostega*, *Acanthostega gunnari*, and the newly described *Hynerpeton bassetti* (Daeschler et al., 1994). (There are also other genera known from more fragmentary fossils.) *Hynerpeton* is the earliest of these three genera (365 Ma), but is more advanced in some ways; the other two genera retained more fish- like characters longer than the *Hynerpeton* lineage did.
- Labyrinthodonts (eg *Pholidogaster*, *Pteroplax*) (late Dev./early Miss.) -- These larger amphibians still have some icthyostegid fish features, such as skull bone patterns, labyrinthine tooth dentine, presence & pattern of large palatal tusks, the fish skull hinge, pieces of gill structure between cheek & shoulder, and the vertebral structure. But they have lost several other fish features: the fin rays in the tail are gone, the vertebrae are stronger and interlocking, the nasal passage for air intake is well defined, etc.

More info on those first known Late Devonian amphibians: *Acanthostega gunnari* was very fish-like, and recently Coates & Clack (1991) found that it still had internal gills! They said: "*Acanthostega* seems to have retained fish-like internal gills and an open opercular chamber for use in aquatic respiration, implying that the earliest tetrapods were not fully terrestrial....Retention of fish-like internal gills by a Devonian tetrapod blurs the traditional distinction between tetrapods and fishes...this adds further support to the suggestion that unique tetrapod characters such as limbs with digits evolved first for use in water rather than for walking on land." *Acanthostega* also had a remarkably fish-like shoulder and forelimb. *Ichthyostega* was also very fishlike, retaining a fish-like finned tail, permanent lateral line system, and notochord. Neither of these two animals could have survived long on land.

Coates & Clack (1990) also recently found the first really well- preserved feet, from *Acanthostega* (front foot found) and *Ichthyostega* (hind foot found). (*Hynerpeton*'s feet are unknown.) The feet were much more fin-like than anyone expected. It had been assumed that they had five toes on each foot, as do all modern tetrapods. This was a puzzle since the fins of lobe-finned fishes don't seem to be built on a five-toed plan. It turns out that *Acanthostega*'s front foot had *eight* toes, and *Ichthyostega*'s hind foot had seven toes, giving both feet the look of a short, stout flipper with many "toe rays" similar to fin rays. All you have to do to a lobe- fin to make it into a many-toed foot like this is curl it, wrapping the fin rays forward around the end of the limb. In fact, this is exactly how feet develop in larval amphibians, from a curled limb bud. (Also see Gould's essay on this subject, "Eight Little Piggies".) Said the discoverers (Coates & Clack, 1990): "The morphology of the limbs of *Acanthostega* and *Ichthyostega* suggest an aquatic mode of life, compatible with a recent assessment of the fish-tetrapod transition. The dorsoventrally compressed lower leg bones of *Ichthyostega* strongly resemble those of a cetacean [whale] pectoral flipper. A peculiar, poorly ossified mass lies anteriorly adjacent to the digits, and appears to be reinforcement for the leading edge of this paddle-like limb." Coates & Clack also found that *Acanthostega*'s front foot couldn't bend forward at the elbow, and thus couldn't be brought into a weight-bearing position. In other words this "foot" still functioned as a horizontal fin. *Ichthyostega*'s hind foot may have functioned this way too, though its *front* feet could take weight. Functionally, these two animals were not fully amphibian; they lived in an in-between fish/amphibian niche, with their feet still partly functioning as fins. Though they are probably not ancestral to later tetrapods, *Acanthostega* & *Ichthyostega* certainly show that the transition from fish to amphibian is feasible!

Hynerpeton, in contrast, probably did not have internal gills and already had a well-developed shoulder girdle; it could elevate and retract its forelimb strongly, and it had strong muscles that attached the shoulder to the rest of the body (Daeschler et al., 1994). *Hynerpeton*'s discoverers think that since it had the strongest limbs earliest on, it may be the actual ancestor of all subsequent terrestrial tetrapods, while *Acanthostega* and *Ichthyostega* may have been a side branch that stayed happily in a mostly-aquatic niche.

In summary, the *very* first amphibians (presently known only from fragments) were probably almost totally aquatic, had both lungs *and* internal gills throughout life, and scudded around underwater with flipper-like, many-toed feet that didn't carry much weight. Different lineages of amphibians began to bend either the hind feet or front feet forward so that the feet carried weight. One line (*Hynerpeton*) bore weight on all four feet, developed strong limb girdles and muscles, and quickly became more terrestrial.

Transitions among amphibians

- Temnospondyls, e.g *Pholidogaster* (Mississippian, about 330 Ma) -- A group of large labrinthodont amphibians, transitional between the early amphibians (the ichthyostegids, described above) and later amphibians such as rhachitomes and anthracosaurs. Probably also gave rise to modern amphibians (the Lissamphibia) via this chain of six temnospondyl genera , showing progressive modification of the palate, dentition, ear, and pectoral girdle, with steady reduction in body size (Milner, in Benton 1988). Notice, though, that the times are out of order, though they are all from the Pennsylvanian and early Permian. Either some of the "Permian" genera arose earlier, in the Pennsylvanian (quite likely), and/or some of these genera are "cousins", not direct ancestors (also quite likely).
- *Dendrerpeton acadianum* (early Penn.) -- 4-toed hand, ribs straight, etc.
- *Archegosaurus decheni* (early Permian) -- Intertemporals lost, etc.
- *Eryops megacephalus* (late Penn.) -- Occipital condyle splitting in 2, etc.
- *Trematops* spp. (late Permian) -- Eardrum like modern amphibians, etc.
- *Amphibamus lyelli* (mid-Penn.) -- Double occipital condyles, ribs very small, etc.
- *Doleserpeton annectens* or perhaps *Schoenfelderpeton* (both early Permian) -- First pedicellate teeth! (a classic trait of modern amphibians) etc.

From there we jump to the Mesozoic:

- *Triadobatrachus* (early Triassic) -- a proto-frog, with a longer trunk and much less specialized hipbone, and a tail still present (but very short).
- *Vieraella* (early Jurassic) -- first known true frog.
- *Karaurus* (early Jurassic) -- first known salamander.

Finally, here's a recently found fossil:

- Unnamed proto-anthracosaur -- described by Bolt et al., 1988. This animal combines primitive features of palaeostegalians (e.g. temnospondyl-like vertebrae) with new anthracosaur-like features. Anthracosaurs were the group of large amphibians that are thought to have led, eventually, to the reptiles. Found in a new Lower Carboniferous site in Iowa, from about 320 Ma.

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Transitional Vertebrate Fossils FAQ
Part 1B

[Last Update: March 17, 1997]

Part 1A Contents Part 2A

Transition from amphibians to amniotes (first reptiles)

The major functional difference between the ancient, large amphibians and the first little reptiles is the amniotic egg. Additional differences include stronger legs and girdles, different vertebrae, and stronger jaw muscles. For more info, see Carroll (1988) and Gauthier et al. (in Benton, 1988)

- *Proterogyrinus* or another early anthracosaur (late Mississippian) -- Classic labyrinthodont-amphibian skull and teeth, but with reptilian vertebrae, pelvis, humerus, and digits. Still has fish skull hinge. Amphibian ankle. 5-toed hand and a 2-3-4-5-3 (almost reptilian) phalangeal count.
- *Limnoscelis*, *Tseajaia* (late Carboniferous) -- Amphibians apparently derived from the early anthracosaurs, but with additional reptilian features: structure of braincase, reptilian jaw muscle, expanded neural arches.
- *Solenodonsaurus* (mid-Pennsylvanian) -- An incomplete fossil, apparently between the anthracosaurs and the cotylosaurs. Loss of palatal fangs, loss of lateral line on head, etc. Still just a single sacral vertebra, though.
- *Hylonomus*, *Paleothyris* (early Pennsylvanian) -- These are protorothyrids, very early cotylosaurs (primitive reptiles). They were quite little, lizard-sized animals with amphibian-like skulls (amphibian pineal opening, dermal bone, etc.), shoulder, pelvis, & limbs, and intermediate teeth and vertebrae. Rest of skeleton reptilian, with reptilian jaw muscle, no palatal fangs, and spool-shaped vertebral centra. Probably no eardrum yet. Many of these new "reptilian" features are also seen in *little* amphibians (which also sometimes have direct-developing eggs laid on land), so perhaps these features just came along with the small body size of the first reptiles.

The ancestral amphibians had a rather weak skull and paired "aortas" (systemic arches). The first reptiles immediately split into two major lines which modified these traits in different ways. One line developed an aorta on the right side and strengthened the skull by swinging the quadrate bone down and forward, resulting in an enormous otic notch (and allowed the later development of good hearing without much further modification). This group further split into three major groups, easily recognizable by the number of holes or "fenestrae" in the side of the skull: the anapsids (no fenestrae), which produced the turtles; the diapsids (two fenestrae), which produced the dinosaurs and birds; and an offshoot group, the eurapsids (two fenestrae fused into one), which produced the ichthyosaurs.

The other major line of reptiles developed an aorta on left side only, and strengthened the skull by moving the quadrate bone up and back, obliterating the otic notch (making involvement of the jaw essential in the later development of good hearing). They developed a single fenestra per side. This group was the synapsid reptiles. They took a radically different path than the other reptiles, involving homeothermy, a larger brain, better hearing and more efficient teeth. One group of synapsids called the "therapsids" took these changes particularly far, and apparently produced the mammals.

Some transitions among reptiles

I will review just a couple of the reptile phylogenies, since there are so many.... Early reptiles to turtles: (Also see Gaffney & Meylan, in Benton 1988)

- *Captorhinus* (early-mid Permain) -- Immediate descendent of the protorothryids.

Here we come to a controversy; there are two related groups of early anapsids, both descended from the captorhinids, that could have been ancestral to turtles. Reisz & Laurin (1991, 1993) believe the turtles descended from procolophonids, late Permian anapsids that had various turtle-like skull features. Others, particularly Lee (1993) think the turtle ancestors are pareiasaurs:

- *Scutosaurus* and other pareiasaurs (mid-Permian) -- Large bulky herbivorous reptiles with turtle-like skull features. Several genera had bony plates in the skin, possibly the first signs of a turtle shell.
- *Deltavjatia vjatkensis* (Permian) -- A recently discovered pareiasaur with numerous turtle-like skull features (e.g., a very high palate), limbs, and girdles, and lateral projections flaring out some of the vertebrae in a very shell-like way. (Lee, 1993)
- *Proganochelys* (late Triassic) -- a primitive turtle, with a fully turtle-like skull, beak, and shell, but with some primitive traits such as rows of little palatal teeth, a still-recognizable clavicle, a simple captorhinid-type jaw musculature, a primitive captorhinid- type ear, a non-retractable neck, etc..
- Recently discovered turtles from the early Jurassic, not yet described.

Mid-Jurassic turtles had already divided into the two main groups of modern turtles, the side-necked turtles and the arch-necked turtles. Obviously these two groups developed neck retraction separately, and came up with totally different solutions. In fact the first known arch-necked turtles, from the Late Jurassic, could not retract their necks, and only later did their descendents develop the archable neck. Early reptiles to diapsids: (see Evans, in Benton 1988, for more info)

- *Hylonomus*, *Paleothyris* (early Penn.) -- The primitive amniotes described above
- *Petrolacosaurus*, *Araeoscelis* (late Pennsylvanian) -- First known diapsids. Both temporal fenestra now present. No significant change in jaw muscles. Have Hylonomus-style teeth, with many small marginal teeth & two slightly larger canines. Still no eardrum.
- *Apsisaurus* (early Permian) -- A more typical diapsid. Lost canines. (Laurin, 1991)

GAP: no diapsid fossils from the mid-Permian.

- *Claudiosaurus* (late Permian) -- An early diapsid with several neodiapsid traits, but still had primitive cervical vertebrae & unossified sternum. probably close to the ancestry of all diapsides (the lizards & snakes & crocs & birds).
- *Planocephalosaurus*(early Triassic) -- Further along the line that produced the lizards and snakes. Loss of some skull bones, teeth, toe bones.
- *Protorosaurus*, *Prolacerta* (early Triassic) -- Possibly among the very first archosaurs, the line that produced dinos, crocs, and birds. May be "cousins" to the archosaurs, though.
- *Proterosuchus* (early Triassic) -- First known archosaur.
- *Hyperodapedon*, *Trilophosaurus* (late Triassic) -- Early archosaurs.

Some species-to-species transitions:

- De Ricqles (in Chaline, 1983) documents several possible cases of gradual evolution (also well as some lineages that showed abrupt appearance or stasis) among the early Permian reptile genera *Captorhinus*, *Protocaptorhinus*, *Eocaptorhinus*, and *Romeria*.
- Horner et al. (1992) recently found many excellent transitional dinosaur fossils from a site in Montana that was a coastal plain in the late Cretaceous. They include:
    1. Many transitional ceratopsids between Styracosaurus and Pachyrhinosaurus
    2. Many transitional lambeosaurids (50! specimens) between Lambeosaurus and Hypacrosaurus.
    3. A transitional pachycephalosaurid between Stegoceras and Pachycephalosaurus
    4. A transitional tyrannosaurid between Tyrannosaurus and Daspletosaurus.

  All of these transitional animals lived during the same brief 500,000 years. Before this site was studied, these dinosaur groups were known from the much larger Judith River Formation, where the fossils showed 5 million years of evolutionary stasis, following by the apparently abrupt appearance of the new forms. It turns out that the sea level rose during that 500,000 years, temporarily burying the Judith River Formation under water, and forcing the dinosaur populations into smaller areas such as the site in Montana. While the populations were isolated in this smaller area, they underwent rapid evolution. When sea level fell again, the new forms spread out to the re-exposed Judith River landscape, thus appearing "suddenly" in the Judith River fossils, with the transitional fossils only existing in the Montana site. This is an excellent example of punctuated equilibrium (yes, 500,000 years is very brief and counts as a "punctuation"), and is a good example of why transitional fossils may only exist in a small area, with the new species appearing "suddenly" in other areas. (Horner et al., 1992) Also note the discovery of *Ianthosaurus*, a genus that links the two synapsid families Ophiacodontidae and Edaphosauridae. (see Carroll, 1988, p. 367)

Transition from synapsid reptiles to mammals

This is the best-documented transition between vertebrate classes. So far this series is known only as a series of genera or families; the transitions from species to species are *not* known. But the family sequence is quite complete. Each group is clearly related to both the group that came before, and the group that came after, and yet the sequence is so long that the fossils at the end are astoundingly different from those at the beginning. As Rowe recently said about this transition (in Szalay et al., 1993), "When sampling artifact is removed and all available character data analyzed [with computer phylogeny programs that do not assume anything about evolution], a highly corroborated, stable phylogeny remains, which is largely consistent with the temporal distributions of taxa recorded in the fossil record." Similarly, Gingerich has stated (1977) "While living mammals are well separated from other groups of animals today, the fossil record clearly shows their origin from a reptilian stock and permits one to trace the origin and radiation of mammals in considerable detail." For more details, see Kermack's superb and readable little book (1984), Kemp's more detailed but older book (1982), and read Szalay et al.'s recent collection of review articles (1993, vol. 1).

This list starts with pelycosaurs (early synapsid reptiles) and continues with therapsids and cynodonts up to the first unarguable "mammal". Most of the changes in this transition involved elaborate repackaging of an expanded brain and special sense organs, remodeling of the jaws & teeth for more efficient eating, and changes in the limbs & vertebrae related to active, legs-under-the-body locomotion. Here are some differences to keep an eye on:

#	Early Reptiles	Mammals
1	No fenestrae in skull	Massive fenestra exposes all of braincase
2	Braincase attached loosely	Braincase attached firmly to skull
3	No secondary palate	Complete bony secondary palate
4	Undifferentiated dentition	Incisors, canines, premolars, molars
5	Cheek teeth uncrowned points	Cheek teeth (PM & M) crowned & cusped
6	Teeth replaced continuously	Teeth replaced once at most
7	Teeth with single root	Molars double-rooted
8	Jaw joint quadrate-articular	Jaw joint dentary-squamosal (*)
9	Lower jaw of several bones	Lower jaw of dentary bone only
10	Single ear bone (stapes)	Three ear bones (stapes, incus, malleus)
11	Joined external nares	Separate external nares
12	Single occipital condyle	Double occipital condyle
13	Long cervical ribs	Cervical ribs tiny, fused to vertebrae
14	Lumbar region with ribs	Lumbar region rib-free
15	No diaphragm	Diaphragm
16	Limbs sprawled out from body	Limbs under body
17	Scapula simple	Scapula with big spine for muscles
18	Pelvic bones unfused	Pelvis fused
19	Two sacral (hip) vertebrae	Three or more sacral vertebrae
20	Toe bone #'s 2-3-4-5-4	Toe bones 2-3-3-3-3

21	Body temperature variable	Body temperature constant

(*) The presence of a dentary-squamosal jaw joint has been arbitrarily selected as the defining trait of a mammal.

- *Paleothyris* (early Pennsylvanian) -- An early captorhinomorph reptile, with no temporal fenestrae at all.
- *Protoclepsydrops haplous* (early Pennsylvanian) -- The earliest known synapsid reptile. Little temporal fenestra, with all surrounding bones intact. Fragmentary. Had amphibian-type vertebrae with tiny neural processes. (reptiles had only just separated from the amphibians)
- *Clepsydrops* (early Pennsylvanian) -- The second earliest known synapsid. These early, very primitive synapsids are a primitive group of pelycosaurs collectively called "ophiacodonts".
- *Archaeothyris* (early-mid Pennsylvanian) -- A slightly later ophiacodont. Small temporal fenestra, now with some reduced bones (supratemporal). Braincase still just loosely attached to skull. Slight hint of different tooth types. Still has some extremely primitive, amphibian/captorhinid features in the jaw, foot, and skull. Limbs, posture, etc. typically reptilian, though the ilium (major hip bone) was slightly enlarged.
- *Varanops* (early Permian) -- Temporal fenestra further enlarged. Braincase floor shows first mammalian tendencies & first signs of stronger attachment to rest of skull (occiput more strongly attached). Lower jaw shows first changes in jaw musculature (slight coronoid eminence). Body narrower, deeper: vertebral column more strongly constructed. Ilium further enlarged, lower-limb musculature starts to change (prominent fourth trochanter on femur). This animal was more mobile and active. Too late to be a true ancestor, and must be a "cousin".
- *Haptodus* (late Pennsylvanian) -- One of the first known sphenacodonts, showing the initiation of sphenacodont features while retaining many primitive features of the ophiacodonts. Occiput still more strongly attached to the braincase. Teeth become size-differentiated, with biggest teeth in canine region and fewer teeth overall. Stronger jaw muscles. Vertebrae parts & joints more mammalian. Neural spines on vertebrae longer. Hip strengthened by fusing to three sacral vertebrae instead of just two. Limbs very well developed.
- *Dimetrodon*, *Sphenacodon* or a similar sphenacodont (late Pennsylvanian to early Permian, 270 Ma) -- More advanced pelycosaurs, clearly closely related to the first therapsids (next). *Dimetrodon* is almost definitely a "cousin" and not a direct ancestor, but as it is known from very complete fossils, it's a good model for sphenacodont anatomy. Medium-sized fenestra. Teeth further differentiated, with small incisors, two huge deep- rooted upper canines on each side, followed by smaller cheek teeth, all replaced continuously. Fully reptilian jaw hinge. Lower jaw bone made of multiple bones & with first signs of a bony prong later involved in the eardrum, but there was no eardrum yet, so these reptiles could only hear ground-borne vibrations (they did have a reptilian middle ear). Vertebrae had still longer neural spines (spectacularly so in *Dimetrodon*, which had a sail), and longer transverse spines for stronger locomotion muscles.
- *Biarmosuchia* (late Permian) -- A therocephalian -- one of the earliest, most primitive therapsids. Several primitive, sphenacodontid features retained: jaw muscles inside the skull, platelike occiput, palatal teeth. New features: Temporal fenestra further enlarged, occupying virtually all of the cheek, with the supratemporal bone completely gone. Occipital plate slanted slightly backwards rather than forwards as in pelycosaurs, and attached still more strongly to the braincase. Upper jaw bone (maxillary) expanded to separate lacrymal from nasal bones, intermediate between early reptiles and later mammals. Still no secondary palate, *but* the vomer bones of the palate developed a backward extension below the palatine bones. This is the first step toward a secondary palate, and with exactly the same pattern seen in cynodonts. Canine teeth larger, dominating the dentition. Variable tooth replacement: some therocephalians (e.g *Scylacosaurus*) had just one canine, like mammals, and stopped replacing the canine after reaching adult size. Jaw hinge more mammalian in position and shape, jaw musculature stronger (especially the mammalian jaw muscle). The amphibian-like hinged upper jaw finally became immovable. Vertebrae still sphenacodontid-like. Radical alteration in the method of locomotion, with a much more mobile forelimb, more upright hindlimb, & more mammalian femur & pelvis. Primitive sphenacodontid humerus. The toes were approaching equal length, as in mammals, with #toe bones varying from reptilian to mammalian. The neck & tail vertebrae became distinctly different from trunk vertebrae. Probably had an eardrum in the lower jaw, by the jaw hinge.
- *Procynosuchus* (latest Permian) -- The first known cynodont -- a famous group of very mammal-like therapsid reptiles, sometimes considered to be the first mammals. Probably arose from the therocephalians, judging from the distinctive secondary palate and numerous other skull characters. Enormous temporal fossae for very strong jaw muscles, formed by just one of the reptilian jaw muscles, which has now become the mammalian masseter. The large fossae is now bounded only by the thin zygomatic arch (cheekbone to

you & me). Secondary palate now composed mainly of palatine bones (mammalian), rather than vomers and maxilla as in older forms; it's still only a partial bony palate (completed in life with soft tissue). Lower incisor teeth was reduced to four (per side), instead of the previous six (early mammals had three). Dentary now is 3/4 of lower jaw; the other bones are now a small complex near the jaw hinge. Jaw hinge still reptilian. Vertebral column starts to look mammalian: first two vertebrae modified for head movements, and lumbar vertebrae start to lose ribs, the first sign of functional division into thoracic and lumbar regions. Scapula beginning to change shape. Further enlargement of the ilium and reduction of the pubis in the hip. A diaphragm may have been present.

- *Dvinia* [also "Permocynodon"] (latest Permian) -- Another early cynodont. First signs of teeth that are more than simple stabbing points -- cheek teeth develop a tiny cusp. The temporal fenestra increased still further. Various changes in the floor of the braincase; enlarged brain. The dentary bone was now the major bone of the lower jaw. The other jaw bones that had been present in early reptiles were reduced to a complex of smaller bones near the jaw hinge. Single occipital condyle splitting into two surfaces. The postcranial skeleton of Dvinia is virtually unknown and it is not therefore certain whether the typical features found at the next level had already evolved by this one. Metabolic rate was probably increased, at least approaching homeothermy.
- *Thrinaxodon* (early Triassic) -- A more advanced "galesaurid" cynodont. Further development of several of the cynodont features seen already. Temporal fenestra still larger, larger jaw muscle attachments. Bony secondary palate almost complete. Functional division of teeth: incisors (four uppers and three lowers), canines, and then 7-9 cheek teeth with cusps for chewing. The cheek teeth were all alike, though (no premolars & molars), did not occlude together, were all single- rooted, and were replaced throughout life in alternate waves. Dentary still larger, with the little quadrate and articular bones were loosely attached. The stapes now touched the inner side of the quadrate. First sign of the mammalian jaw hinge, a ligamentous connection between the lower jaw and the squamosal bone of the skull. The occipital condyle is now two slightly separated surfaces, though not separated as far as the mammalian double condyles. Vertebral connections more mammalian, and lumbar ribs reduced. Scapula shows development of a new mammalian shoulder muscle. Ilium increased again, and all four legs fully upright, not sprawling. Tail short, as is necessary for agile quadrupedal locomotion. The whole locomotion was more agile. Number of toe bones is 2.3.4.4.3, intermediate between reptile number (2.3.4.5.4) and mammalian (2.3.3.3.3), and the "extra" toe bones were tiny. Nearly complete skeletons of these animals have been found curled up - a possible reaction to conserve heat, indicating possible endothermy? Adults and juveniles have been found together, possibly a sign of parental care. The specialization of the lumbar area (e.g. reduction of ribs) is indicative of the presence of a diaphragm, needed for higher O2 intake and homeothermy. NOTE on hearing: The eardrum had developed in the only place available for it -- the *lower* jaw, right near the jaw hinge, supported by a wide prong (reflected lamina) of the angular bone. These animals could now hear airborne sound, transmitted through the eardrum to two small lower jaw bones, the articular and the quadrate, which contacted the stapes in the skull, which contacted the cochlea. Rather a roundabout system and sensitive to low-frequency sound only, but better than no eardrum at all! Cynodonts developed quite loose quadrates and articulars that could vibrate freely for sound transmittal while still functioning as a jaw joint, strengthened by the mammalian jaw joint right next to it. All early mammals from the Lower Jurassic have this low-frequency ear and a double jaw joint. By the middle Jurassic, mammals lost the reptilian joint (though it still occurs briefly in embryos) and the two bones moved into the nearby middle ear, became smaller, and became much more sensitive to high-frequency sounds.
- *Cynognathus* (early Triassic, 240 Ma; suspected to have existed even earlier) -- We're now at advanced cynodont level. Temporal fenestra larger. Teeth differentiating further; cheek teeth with cusps met in true occlusion for slicing up food, rate of replacement reduced, with mammalian-style tooth roots (though single roots). Dentary still larger, forming 90% of the muscle-bearing part of the lower jaw. TWO JAW JOINTS in place, mammalian and reptilian: A new bony jaw joint existed between the squamosal (skull) and the surangular bone (lower jaw), while the other jaw joint bones were reduced to a compound rod lying in a trough in the dentary, close to the middle ear. Ribs more mammalian. Scapula halfway to the mammalian condition. Limbs were held under body. There is possible evidence for fur in fossil pawprints.
- *Diademodon* (early Triassic, 240 Ma; same strata as *Cynognathus*) -- Temporal fenestra larger still, for still stronger jaw muscles. True bony secondary palate formed exactly as in mammals, but didn't extend quite as far back. Turbinate bones possibly present in the nose (warm-blooded?). Dental changes continue: rate of tooth replacement had decreased, cheek teeth have better cusps & consistent wear facets (better occlusion). Lower jaw almost entirely dentary, with tiny articular at the hinge. Still a double jaw joint. Ribs shorten suddenly in lumbar region, probably improving diaphragm function & locomotion. Mammalian toe bones (2.3.3.3.3), with closely related species still showing variable numbers.
- *Probelesodon* (mid-Triassic; South America) -- Fenestra very large, still separate from eyesocket (with

postorbital bar). Secondary palate longer, but still not complete. Teeth double-rooted, as in mammals. Nares separated. Second jaw joint stronger. Lumbar ribs totally lost; thoracic ribs more mammalian, vertebral connections very mammalian. Hip & femur more mammalian.

- *Probainognathus* (mid-Triassic, 239-235 Ma, Argentina) -- Larger brain with various skull changes: pineal foramen ("third eye") closes, fusion of some skull plates. Cheekbone slender, low down on the side of the eye socket. Postorbital bar still there. Additional cusps on cheek teeth. Still two jaw joints. Still had cervical ribs & lumbar ribs, but they were very short. Reptilian "costal plates" on thoracic ribs mostly lost. Mammalian #toe bones.
- *Exaeretodon* (mid-late Triassic, 239Ma, South America) -- (Formerly lumped with the herbivorous gomphodont cynodonts.) Mammalian jaw prong forms, related to eardrum support. Three incisors only (mammalian). Costal plates completely lost. More mammalian hip related to having limbs under the body. Possibly the first steps toward coupling of locomotion & breathing. This is probably a "cousin" fossil not directly ancestral, as it has several new but non-mammalian teeth traits.

GAP of about 30 my in the late Triassic, from about 239-208 Ma. Only one early mammal fossil is known from this time. The next time fossils are found in any abundance, tritylodontids and trithelodontids had already appeared, leading to some very heated controversy about their relative placement in the chain to mammals. Recent discoveries seem to show trithelodontids to be more mammal- like, with tritylodontids possibly being an offshoot group (see Hopson 1991, Rowe 1988, Wible 1991, and Shubin et al. 1991). Bear in mind that both these groups were almost fully mammalian in every feature, lacking only the final changes in the jaw joint and middle ear.

- *Oligokyphus*, *Kayentatherium* (early Jurassic, 208 Ma) -- These are tritylodontids, an advanced cynodont group. Face more mammalian, with changes around eyesocket and cheekbone. Full bony secondary palate. Alternate tooth replacement with double-rooted cheek teeth, but *without* mammalian-style tooth occlusion (which some earlier cynodonts already had). Skeleton strikingly like egg- laying mammals (monotremes). Double jaw joint. More flexible neck, with mammalian atlas & axis and double occipital condyle. Tail vertebrae simpler, like mammals. Scapula is now substantially mammalian, and the forelimb is carried directly under the body. Various changes in the pelvis bones and hind limb muscles; this animal's limb musculature and locomotion were virtually fully mammalian. Probably cousin fossils (?), with *Oligokyphus* being more primitive than *Kayentatherium*. Thought to have diverged from the trithelodontids during that gap in the late Triassic. There is disagreement about whether the tritylodontids were ancestral to mammals (presumably during the late Triassic gap) or whether they are a specialized offshoot group not directly ancestral to mammals.
- *Pachygenelus*, *Diarthrognathus* (earliest Jurassic, 209 Ma) -- These are trithelodontids, a slightly different advanced cynodont group. New discoveries (Shubin et al., 1991) show that these animals are very close to the ancestry of mammals. Inflation of nasal cavity, establishment of Eustachian tubes between ear and pharynx, loss of postorbital bar. Alternate replacement of mostly single- rooted teeth. This group also began to develop double tooth roots -- in *Pachygenelus* the single root of the cheek teeth begins to split in two at the base. *Pachygenelus* also has mammalian tooth enamel, and mammalian tooth occlusion. Double jaw joint, with the second joint now a dentary-*squamosal* (instead of surangular), fully mammalian. Incipient dentary condyle. Reptilian jaw joint still present but functioning almost entirely in hearing; postdentary bones further reduced to tiny rod of bones in jaw near middle ear; probably could hear high frequencies now. More mammalian neck vertebrae for a flexible neck. Hip more mammalian, with a very mammalian iliac blade & femur. Highly mobile, mammalian-style shoulder. Probably had coupled locomotion & breathing. These are probably "cousin" fossils, not directly ancestral (the true ancestor is thought to have occurred during that late Triassic gap). *Pachygenelus* is pretty close, though.
- *Adelobasileus cromptoni* (late Triassic; 225 Ma, west Texas) -- A recently discovered fossil proto-mammal from right in the middle of that late Triassic gap! Currently the oldest known "mammal." Only the skull was found. "Some cranial features of *Adelobasileus*, such as the incipient promontorium housing the cochlea, represent an intermediate stage of the character transformation from non-mammalian cynodonts to Liassic mammals" (Lucas & Luo, 1993). This fossil was found from a band of strata in the western U.S. that had not previously been studied for early mammals. Also note that this fossil dates from slightly *before* the known tritylodonts and trithelodonts, though it has long been suspected that tritilodonts and trithelodonts were already around by then. *Adelobasileus* is thought to have split off from either a trityl. or a trithel., and is either identical to or closely related to the common ancestor of all mammals.
- *Sinoconodon* (early Jurassic, 208 Ma) -- The next known very ancient proto-mammal. Eyesocket fully mammalian now (closed medial wall). Hindbrain expanded. Permanent cheekteeth, like mammals, but the other teeth were still replaced several times. Mammalian jaw joint stronger, with large dentary condyle fitting into a distinct fossa on the squamosal. This final refinement of the joint automatically makes this

animal a true "mammal". Reptilian jaw joint *still* present, though tiny.

- *Kuehneotherium* (early Jurassic, about 205 Ma) -- A slightly later proto-mammal, sometimes considered the first known pantothere (primitive placental-type mammal). Teeth and skull like a placental mammal. The three major cusps on the upper & lower molars were rotated to form interlocking shearing triangles as in the more advanced placental mammals & marsupials. Still has a double jaw joint, though.
- *Eozostrodon*, *Morganucodon*, *Haldanodon* (early Jurassic, ~205 Ma) -- A group of early proto-mammals called "morganucodonts". The restructuring of the secondary palate and the floor of the braincase had continued, and was now very mammalian. Truly mammalian teeth: the cheek teeth were finally differentiated into simple premolars and more complex molars, and teeth were replaced only once. Triangular- cusped molars. Reversal of the previous trend toward reduced incisors, with lower incisors increasing to four. Tiny remnant of the reptilian jaw joint. Once thought to be ancestral to monotremes only, but now thought to be ancestral to all three groups of modern mammals -- monotremes, marsupials, and placentals.
- *Peramus* (late Jurassic, about 155 Ma) -- A "eupantothere" (more advanced placental-type mammal). The closest known relative of the placentals & marsupials. Triconodont molar has with more defined cusps. This fossil is known only from teeth, but judging from closely related eupantotheres (e.g. *Amphitherium*) it had finally lost the reptilian jaw joint, attaing a fully mammalian three-boned middle ear with excellent high-frequency hearing. Has only 8 cheek teeth, less than other eupantotheres and close to the 7 of the first placental mammals. Also has a large talonid on its "tribosphenic" molars, almost as large as that of the first placentals -- the first development of grinding capability.
- *Endotherium* (very latest Jurassic, 147 Ma) -- An advanced eupantothere. Fully tribosphenic molars with a well- developed talonid. Known only from one specimen. From Asia; recent fossil finds in Asia suggest that the tribosphenic molar evolved there.
- *Kielantherium* and *Aegialodon* (early Cretaceous) -- More advanced eupantotheres known only from teeth. *Kielantherium* is from Asia and is known from slightly older strata than the European *Aegialodon*. Both have the talonid on the lower molars. The wear on it indicates that a major new cusp, the protocone, had evolved on the upper molars. By the Middle Cretaceous, animals with the new tribosphenic molar had spread into North America too (North America was still connected to Europe.)
- *Steropodon galmani* (early Cretaceous) -- The first known definite monotreme, discovered in 1985.
- *Vincelestes neuquenianus* (early Cretaceous, 135 Ma) -- A probably-placental mammal with some marsupial traits, known from some nice skulls. Placental-type braincase and coiled cochlea. Its intracranial arteries & veins ran in a composite monotreme/placental pattern derived from homologous extracranial vessels in the cynodonts. (Rougier et al., 1992)
- *Pariadens kirklandi* (late Cretaceous, about 95 Ma) -- The first definite marsupial. Known only from teeth.
- *Kennalestes* and *Asioryctes* (late Cretaceous, Mongolia) -- Small, slender animals; eyesocket open behind; simple ring to support eardrum; primitive placental-type brain with large olfactory bulbs; basic primitive tribosphenic tooth pattern. Canine now double rooted. Still just a trace of a non-dentary bone, the coronoid, on the otherwise all-dentary jaw. "Could have given rise to nearly all subsequent placentals." says Carroll (1988).
- *Cimolestes*, *Procerberus*, *Gypsonictops* (very late Cretaceous) -- Primitive North American placentals with same basic tooth pattern.

So, by the late Cretaceous the three groups of modern mammals were in place: monotremes, marsupials, and placentals. Placentals appear to have arisen in East Asia and spread to the Americas by the end of the Cretaceous. In the latest Cretaceous, placentals and marsupials had started to diversify a bit, and after the dinosaurs died out, in the Paleocene, this diversification accelerated. For instance, in the mid- Paleocene the placental fossils include a very primitive primate-like animal (*Purgatorius* - known only from a tooth, though, and may actually be an early ungulate), a herbivore-like jaw with molars that have flatter tops for better grinding (*Protungulatum*, probably an early ungulate), and an insectivore (*Paranyctoides*).

The decision as to which was the first mammal is somewhat subjective. We are placing an inflexible classification system on a gradational series. What happened was that an intermediate group evolved from the 'true' reptiles, which gradually acquired mammalian characters until a point was reached where we have artificially drawn a line between reptiles and mammals. For instance, *Pachygenulus* and *Kayentatherium* are both far more mammal-like than reptile-like, but they are both called "reptiles".

Transition from diapsid reptiles to birds

In the mid-1800's, this was one of the most significant gaps in vertebrate fossil evolution. No transitional fossils at all were known, and the two groups seemed impossibly different. Then the exciting discovery of *Archeopteryx* in 1861 showed clearly that the two groups were in fact related. Since then, some other reptile-bird links have been found. On the whole, though, this is still a gappy transition, consisting of a very large-scale series of "cousin" fossils. I have not included *Mononychus* (as it appears to be a digger, not a flier, well off the line to modern birds). See Feduccia (1980) and Rayner (1989) for more discussion of the evolution of flight, and Chris Nedin's excellent Archeopteryx FAQ for more info on that critter.

- *Coelophysis* (late Triassic) -- One of the first theropod dinosaurs. Theropods in general show clear general skeletal affinities with birds (long limbs, hollow bones, foot with 3 toes in front and 1 reversed toe behind, long ilium). Jurassic theropods like *Compsognathus* are particularly similar to birds.
- *Deinonychus*, *Oviraptor*, and other advanced theropods (late Jurassic, Cretaceous) -- Predatory bipedal advanced theropods, larger, with more bird-like skeletal features: semilunate carpal, bony sternum, long arms, reversed pubis. Clearly runners, though, not fliers. These advanced theropods even had clavicles, sometimes fused as in birds. Says Clark (1992): "The detailed similarity between birds and theropod dinosaurs such as *Deinonychus* is so striking and so pervasive throughout the skeleton that a considerable amount of special pleading is needed to come to any conclusion other than that the sister-group of birds among fossils is one of several theropod dinosaurs." The particular fossils listed here are are *not* directly ancestral, though, as they occur after *Archeopteryx*.
- *Lisboasaurus estesi* & other "troodontid dinosaur-birds" (mid-Jurassic) -- A bird-like theropod reptile with very bird-like teeth (that is, teeth very like those of early toothed birds, since modern birds have no teeth). These really could be ancestral.

GAP: The exact reptilian ancestor of *Archeopteryx*, and the first development of feathers, are unknown. Early bird evolution seems to have involved little forest climbers and then little forest fliers, both of which are guaranteed to leave very bad fossil records (little animal + acidic forest soil = no remains). *Archeopteryx* itself is really about the best we could ask for: several specimens has superb feather impressions, it is *clearly* related to both reptiles and birds, and it *clearly* shows that the transition is feasible.

- One possible ancestor of *Archeopteryx* is *Protoavis* (Triassic, ~225 Ma) -- A highly controversial fossil that may or may not be an extremely early bird. Unfortunately, not enough of the fossil was recovered to determine if it is definitely related to the birds.
- *Archeopteryx lithographica* (Late Jurassic, 150 Ma) -- The several known specimes of this deservedly famous fossil show a mosaic of reptilian and avian features, with the reptilian features predominating. The skull and skeleton are basically reptilian (skull, teeth, vertebrae, sternum, ribs, pelvis, tail, digits, claws, generally unfused bones). Bird traits are limited to an avian furcula (wishbone, for attachment of flight muscles; recall that at least some dinosaurs had this too), modified forelimbs, and -- the real kicker -- unmistakable lift-producing flight feathers. *Archeopteryx* could probably flap from tree to tree, but couldn't take off from the ground, since it lacked a keeled breastbone for large flight muscles, and had a weak shoulder compared to modern birds. May not have been the direct ancestor of modern birds. (Wellnhofer, 1993)
- *Sinornis santensis* ("Chinese bird", early Cretaceous, 138 Ma) -- A recently found little primitive bird. Bird traits: short trunk, claws on the toes, flight-specialized shoulders, stronger flight- feather bones, tightly folding wrist, short hand. (These traits make it a much better flier than *Archeopteryx*.) Reptilian traits: teeth, stomach ribs, unfused hand bones, reptilian-shaped unfused pelvis. (These remaining reptilian traits wouldn't have interfered with flight.) Intermediate traits: metatarsals partially fused, medium-sized sternal keel, medium-length tail (8 vertebrae) with fused pygostyle at the tip. (Sereno & Rao, 1992).
- "Las Hoyas bird" or "Spanish bird" [not yet named; early Cretaceous, 131 Ma) -- Another recently found "little forest flier". It still has reptilian pelvis & legs, with bird-like shoulder. Tail is medium-length with a fused tip. A fossil down feather was found with the Las Hoyas bird, indicating homeothermy. (Sanz et al., 1992)
- *Ambiortus dementjevi* (early Cretaceous, 125 Ma) -- The third known "little forest flier", found in 1985. Very fragmentary fossil.
- *Hesperornis*, *Ichthyornis*, and other Cretaceous diving birds -- This line of birds became specialized for diving, like modern cormorants. As they lived along saltwater coasts, there are many fossils known. Skeleton further modified for flight (fusion of pelvis bones, fusion of hand bones, short & fused tail). Still had true socketed teeth, a reptilian trait.

[Note: a classic study of chicken embryos showed that chicken bills can be induced to develop teeth, indicating that chickens (and perhaps other modern birds) still retain the genes for making teeth. Also note that molecular data shows that crocodiles are birds' closest living relatives.]

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Transitional Vertebrate Fossils FAQ
Part 2A

[Last Update: March 17, 1997]

Part 1B Contents Part 2B

PART 2

Overview of the Cenozoic

The Cenozoic fossil record is much better than the older Mesozoic record, and *much* better than the very much older Paleozoic record. The most extensive Cenozoic gaps are early on, in the Paleocene and in the Oligocene. From the Miocene on it gets better and better, though it's still never perfect. Not surprisingly, the very recent Pleistocene has the best record of all, with the most precisely known lineages and most of the known species-to-species transitions. For instance, of the 111 modern mammal species that appeared in Europe during the Pleistocene, at least 25 can be linked to earlier European ancestors by species-to-species transitional morphologies (see Kurten, 1968, and Barnosky, 1987, for discussion).

Timescale

Pleistocene	2.5-0.01 Ma	Excellent mammal record
Pliocene	5.3-2.5 Ma	Very good mammal record
Miocene	24-5.3 Ma	Pretty good mammal record
Oligocene	34-24 Ma	Spotty mammal record. Many gaps in various lineages
Eocene	54-34 Ma	Surprisingly good mammal record, due to uplift and exposure of fossil-bearing strata in the Rockies
Paleocene	67-54 Ma	Fair record early on, but late Paleocene is lousy

For the rest of this FAQ, I'll walk through the known fossil records for the major orders of modern placental mammals. For each order, I'll describe the known lineages leading from early unspecialized placentals to the modern animals, point out some of the remaining gaps, and list several of the known species-to-species transitions. I left out some of the obscure orders (e.g. hyraxes, anteaters), groups that went completely extinct, and some of the families of particularly diverse orders.

Primates

I'll outline here the lineage that led to humans. Notice that there were many other large, successful branches (particularly the lemurs, New World monkeys, and Old World monkeys) that I will only mention in passing. Also see Jim Foley's fossil hominid FAQ for detailed information on hominid fossils.

GAP: "The modern assemblage can be traced with little question to the base of the Eocene" says Carroll (1988). But before that, the origins of the very earliest primates are fuzzy. There is a group of Paleocene primitive primate-like animals called "plesiadapids" that may be ancestral to primates, or may be "cousins" to primates. (see Beard, in Szalay et al., 1993.)

- *Palaechthon*, *Purgatorius* (middle Paleocene) -- Very primitive plesiadapids. To modern eyes they looks nothing like primates, being simply pointy-faced, small early mammals with mostly primitive teeth, and claws instead of nails. But they show the first signs of primate-like teeth; lost an incisor and a premolar, and had relatively blunt-cusped, squarish molars.
- *Cantius* (early Eocene) -- One of the first true primates (or "primates of modern aspect"), more advanced than the plesiadapids (more teeth lost, bar behind the eye, grasping hand & foot) and beginning to show some lemur-like arboreal adaptations.
- *Pelycodus* & related species (early Eocene) -- Primitive lemur-like primates.

The tarsiers, lemurs, and New World monkeys split off in the Eocene. The Old World lineage continued as follows:

- *Amphipithecus*, *Pondaungia* (late Eocene, Burma) -- Very early Old World primates known only from fragments. Larger brain, shorter nose, more forward-facing eyes (halfway between plesiadapid eyes and modern ape eyes).

GAP: Here's that Oligocene gap mentioned above in the timescale. Very few primate fossils are known between the late Eocene and early Oligocene, when there was a sharp change in global climate. Several other mammal groups have a similar gap.

- *Parapithecus* (early Oligocene) -- The O.W. monkeys split from the apes split around now. *Parapithecus* was probably at the start of the O.W. monkey line. From here the O.W. monkeys go through *Oreopithecus* (early Miocene, Kenya) to modern monkey groups of the Miocene & Pliocene.
- *Propliopithecus*, *Aegyptopithecus* (early Oligocene, Egypt) -- From the same time as *Parapithecus*, but probably at the beginning of the ape lineage. First ape characters (deep jaw, 2 premolars, 5- cusped teeth, etc.).
- *Aegyptopithecus* (early-mid Oligocene, Egypt) -- Slightly later anthropoid (ape/hominid) with more ape features. It was a fruit-eating runner/climber, larger, with a rounder brain and shorter face.
- *Proconsul africanus* (early Miocene, Kenya.) -- A sexually dimorphic, fruit-eating, arboreal quadruped probably ancestral to all the later apes and humans. Had a mosaic of ape-like and primitive features; Ape-like elbow, shoulder and feet; monkey- like wrist; gibbon-like lumbar vertebrae.
- *Limnopithecus* (early Miocene, Africa) -- A later ape probably ancestral to gibbons.
- *Dryopithecus* (mid-Miocene) -- A later ape probably ancestral to the great apes & humans. At this point Africa & Asia connected via Arabia, and the non-gibbon apes divided into two lines:
    1. *Sivapithecus* (including "Gigantopithecus" & "Ramapithecus", mid- Miocene) -- Moved to Asia & gave rise to the orangutan.
    2. *Kenyapithecus* (mid-Miocene, about 16 Ma) -- Stayed in Africa & gave rise to the African great apes & humans.

GAP: There are no known fossil hominids *or* apes from Africa between 14 and 4 Ma. Frustratingly, molecular data shows that this is when the African great apes (chimps, gorillas) diverged from hominids, probably 5-7 Ma. The gap may be another case of poor fossilization of forest animals. At the end of the gap we start finding some very ape-like bipedal hominids:

- *Australopithecus ramidus* (mid-Pliocene, 4.4 Ma) -- A recently discovered very early hominid (or early chimp?), from just after the split with the apes. Not well known. Possibly bipedal (only the skull was found). Teeth both apelike and humanlike; one baby tooth is very chimp-like. (White et al., 1994; Wood 1994)
- *Australopithecus afarensis* (late Pliocene, 3.9 Ma) -- Some excellent fossils ("Lucy", etc.) make clear that this was fully bipedal and definitely a hominid. But it was an extremely ape-like hominid; only four feet tall, still had an ape-sized brain of just 375-500 cc (finally answering the question of which came first, large

brain or bipedality) and ape-like teeth. This lineage gradually split into a husky large-toothed lineage and a more slender, smaller- toothed lineage. The husky lineage (A. robustus, A. boisei) eventually went extinct.

- *Australopithecus africanus* (later Pliocene, 3.0 Ma) -- The more slender lineage. Up to five feet tall, with slightly larger brain (430-550 cc) and smaller incisors. Teeth gradually became more and more like *Homo* teeth. These hominds are almost perfect ape- human intermediates, and it's now pretty clear that the slender australopithecines led to the first *Homo* species.
- *Homo habilis* (latest Pliocene/earliest Pleistocene, 2.5 Ma) -- Straddles the boundary between australopithecines and humans, such that it's sometimes lumped with the australopithecines. About five feet tall, face still primitive but projects less, molars smaller. Brain 500-800 cc, overlapping australopithecines at the low end and and early Homo erectus at the high end. Capable of rudimentary speech? First clumsy stone tools.
- *Homo erectus* (incl. "Java Man", "Peking Man", "Heidelberg Man"; Pleist., 1.8 Ma) -- Looking much more human now with a brain of 775-1225 cc, but still has thick brow ridges & no chin. Spread out of Africa & across Europe and Asia. Good tools, first fire.
- Archaic *Homo sapiens* (Pleistocene, 500,000 yrs ago) -- These first primitive humans were perfectly intermediate between H. erectus and modern humans, with a brain of 1200 cc and less robust skeleton & teeth. Over the next 300,000 years, brain gradually increased, molars got still smaller, skeleton less muscular. Clearly arose from *H erectus*, but there are continuing arguments about where this happened.
- One famous offshoot group, the Neandertals, developed in Europe 125,000 years ago. They are considered to be the same species as us, but a different subspecies, *H. sapiens neandertalensis*. They were more muscular, with a slightly *larger* brain of 1450 cc, a distinctive brow ridge, and differently shaped throat (possibly limiting their language?). They are known to have buried their dead.
- *H. sapiens sapiens* (incl. "Cro-magnons"; late Pleist., 40,000 yrs ago) -- All modern humans. Average brain size 1350 cc. In Europe, gradually supplanted the Neanderthals.

Known species-species transitions in primates:

Phillip Gingerich has done a lot of work on early primate transitions. Here are some of his major findings in plesiadapids, early lemurs, and early monkeys:

- Plesiadapids: Gingerich (summarized in 1976, 1977) found smooth transitions in plesiadapid primates linking four genera together: *Pronothodectes*, *Nannodectes*, two lineages of *Plesiadapis*, and *Platychoerops*. In summary: *Pronothodectes matthewi* changed to become *Pro. jepi*, which split into *Nannodectes intermedius* and *Plesiadapis praecursor*. *N. intermedius* was the first member of a gradually changing lineage that passed through three different species stages (N. gazini, N. simpsoni, and N. gidleyi). *Ples. praecursor* was the first member of a separate, larger lineage that slowly grew larger (passing through three more species stages), with every studied character showing continuous gradual change. Gingerich (1976) noted "Loss of a tooth, a discrete jump from one state to another, in several instances proceeded continuously by continuous changes in the frequencies of dimorphism -- the percentage of specimens retaining the tooth gradually being reduced until it was lost entirely from the population." The Plesiadapis lineage then split into two more lineages, each with several species. One of these lineages shows a gradual transition from *Plesiadapis* to *Platychoerops*,"where the incisors were considerably reorganized morphologically and functionally in the space of only 2-3 million years."
- Early lemur-like primates: Gingerich (summarized in 1977) traced two distinct species of lemur-like primates, *Pelycodus frugivorus* and *P. jarrovii*, back in time, and found that they converged on the earlier *Pelycodus abditus* "in size, mesostyle development, and every other character available for study, and there can be little doubt that each was derived from that species." Further work (Gingerich, 1980) in the same rich Wyoming fossil sites found species-to-species transitions for *every step* in the following lineage: *Pelycodus ralstoni* (54 Ma) to *P. mckennai* to *P. trigonodus* to *P. abditus*, which then forked into three branches. One became a new genus, *Copelemur feretutus*, and further changed into *C. consortutus*. The second branch became *P. frugivorus*. The third led to *P. jarrovi*, which changed into another new genus, *Notharctus robinsoni*, which itself split into at least two branches, *N. tenebrosus*, and *N. pugnax* (which then changed to *N. robustior*, 48 Ma), and possibly a third, *Smilodectes mcgrewi* (which then changed to *S. gracilis*). Note that this sequence covers *at least* three and possibly four genera, with a timespan of 6 million years.
- Early monkey-like primates: Gingerich (1982, also discussed in Gingerich, 1983) also describes gradual species-species transitions in a lineage of early Eocene primate: *Cantius ralstoni* to *C. mckennai* to *C. trigonodus*.

And here are some transitions found by other researchers:

- Rose & Bown (1984) analyzed over 600 specimens of primates collected from a 700-meter-thick sequence representing approximately 4 million years of the Eocene. They found smooth transitions between *Teilhardina americana* and *Tetonoides tenuiculus*, and also beween *Tetonius homunculus* and *Pseudotetonius ambiguus*. "In both lines transitions occurred not only continuously (rather than by abrupt appearance of new morphologies followed by stasis), but also in mosaic fashion, with greater variation in certain characters preceding a shift to another character state." The *T. homunculus - P. ambiguus* transition shows a dramatic change in dentition (loss of P2, dramatic shrinkage of P3 with loss of roots, shrinkage of C and I2, much enlarged I1) that occurs gradually and smoothly during the 4 million years. The authors conclude "...our data suggest that phyletic gradualism is not only more common than some would admit but also capable of producing significant adaptive modifications."
- Delson (discussed in Gingerich, 1985) has studied transitions in primates from the Miocene to the present. For instance, in a 1983 paper (see Chaline, 1983), he discussed a possible smooth transition from *Theropithecus darti* to *T. oswaldi*, and discusses transitions in hominids, concluding that *Homo sapiens* clearly shows gradual changes over the last 800,000 years.
- Kurten (1968) reports a smooth transition linking *Macaca florentina* to *M. sylvana*

Bats

GAP: One of the least understood groups of modern mammals -- there are no known bat fossils from the entire Paleocene. The first known fossil bat, *Icaronycteris*, is from the (later) Eocene, and it was already a fully flying animal very similar to modern bats. It did still have a few "primitive" features, though (unfused & unkeeled sternum, several teeth that modern bats have lost, etc.)

- Fruit bats and horseshoe bats first appear in the Oligocene. Modern little vespertiliontids (like the little brown bat) first appear in the Miocene.

Carnivores

- Creodonts -- early placental mammals with minor but interestingly carnivore-like changes in the molars and premolars. Had a carnivore- like shearing zone in the teeth, though the zone moved throughout life instead of staying in particular teeth. Also had a carnivore- like bony sheet in the brain dividing cerebrum & cerebellum, details of ankle. Closely related to & possibly ancestral to carnivores. The origin of the creodonts is unclear. They probably were derived from condylarths.
- *Cimolestes* (late Cretaceous) -- This creodont (?) lost the last molar & then later enlarged the last upper premolar and first lower molar. (In modern carnivores, these two teeth are very enlarged to be the wickedly shearing carnassial teeth, the hallmark of carnivores.) Still unfused feet & unossified bulla. This genus is probably ancestral to two later lines of Eocene carnivores called "miacoids". Miacoids were relatively unspecialized meat-eaters that seem to have split into a "viverravid" line (with cat/civet/hyena traits) and a "miacid" line (with dog/bear/weasel traits). These two lines may possibly have arisen from these slightly different species of *Cimolestes*:
- *Cimolestes incisus* & *Cimolestes cerberoides* (Cretaceous) -- These are two species that lost their third molar, and may have given rise to the viverravid line of miacoids (see Hunt & Tedford, in Szalay et al., 1993).
- *Cimolestes sp.* (Paleocene) -- A later, as yet unnamed species that has very miacid-like teeth.
- *Simpsonictis tenuis* (mid-Paleocene) -- A very early viverravid. The upper carnassial was large; the lower carnassial was of variable size in different individuals.
- *Paroodectes*, *Vulpavus* (early Eocene) -- Early miacids. Enlarged carnassials now specialized for shearing. Still had unfused foot bones, short limbs, plantigrade feet, unossified bulla.

GAP: few miacoid skulls are known from the rest of the Eocene -- a real pity because for early carnivore relationships, skulls (particularly the skull floor and ear capsule) are more useful than teeth. There are some later skulls from the early Oligocene, which are already distinguishable as canids, viverrids, mustelids, & felids (a dog-like face, a cat-like face, and so on). Luckily some new well-preserved miacoid fossils have just been found in the last few years (mentioned in Szalay et al., 1993). They are still being studied and will probably clarify exactly which miacoids gave rise to which carnivores. Meanwhile, analysis of teeth has revealed at least one ancestor:

- *Viverravus sicarius* (mid-Eocene) -- Hunt & Tedford (in Szalay et al., 1993) think this viverravid may be the ancestral aeluroid. It has teeth & skeletal traits similar to the first known Oligocene aeluroids (undifferentiated cat/civet/hyenas).

From the Oligocene onward, the main carnivore lineages continued to diverge. First, the dog/bear/weasel line.

Dogs:

- *Cynodictis* (late Eocene) -- First known arctoid (undifferentiated dog/bear).
- *Hesperocyon* (early Oligocene) -- A later arctoid. Compared to miacids like *Paroodectes*, limbs have elongated, carnassials are more specialized, braincase is larger. From here, the main line of canid evolution can be traced in North America, with bears branching out into a Holarctic distribution.
- *Cynodesmus* (Miocene) -- First true dog. The dog lineage continued through *Tomarctus* (Pliocene) to the modern dogs, wolves, & foxes, *Canis* (Pleistocene).

Bears:

- *Cynodictis* (see above)
- *Hesperocyon* (see above)
- *Ursavus elmensis* (mid-Oligocene) -- A small, heavy doglike animal, intermediate between arctoids and bears. Still had slicing carnassials & all its premolars, but molars were becoming squarer. Later specimens of *Ursavus* became larger, with squarer, more bear-like, molars.
- *Protursus simpsoni* (Pliocene; also "Indarctos") -- Sheepdog-sized. Carnassial teeth have no shearing action, molars are square, shorter tail, heavy limbs. Transitional to the modern genus *Ursus*.
- *Ursus minimus* (Pliocene) -- First little bear, with very bearlike molars, but still had the first premolars and slender canines. Shows gradual tooth changes and increase in body size as the ice age approached. Gave rise to the modern black bears (*U. americanus* & *U. thibetanus*), which haven't changed much since the Pliocene, and also smoothly evolved to the next species, *U. etruscus*:
- *Ursus etruscus* (late Pliocene) -- A larger bear, similar to our brown bear but with more primitive dentition. Molars big & square. First premolars small, and got smaller over time. Canines stouter. In Europe, gradually evolved into:
- *Ursus savini* (late Pleistocene, 1 Ma) -- Very similar to the brown bear. Some individuals didn't have the first premolars at all, while others had little vestigial premolars. Tendency toward domed forehead. Slowly split into a European population and an Asian population.
- *U. spelaeus* (late Pleistocene) -- The recently extinct giant cave bear, with a highly domed forehead. Clearly derived from the European population of U. savini, in a smooth transition. The species boundary is arbitrarily set at about 300,000 years ago.
- *U. arctos* (late Pleistocene) -- The brown ("grizzly") bear, clearly derived from the Asian population of *U. savini* about 800,000 years ago.. Spread into the Europe, & to the New World.
- *U. maritimus* (late Pleistocene) -- The polar bear. Very similar to a local population of brown bear, *U. arctos beringianus* that lived in Kamchatka about 500,000 years ago (Kurten 1964).

The transitions between each of these bear species are very well documented. For most of the transitions there are superb series of transitional specimens leading right across the species "boundaries". See Kurten (1976) for basic info on bear evolution.

Raccoons (procyonids):

- *Phlaocyon* (Miocene) -- A climbing carnivore with non-shearing carnassials and handlike forepaws, transitional from the arctoids to the procyonids (raccoons et al.). Typical raccoons first appeared in the Pliocene.

Weasels (mustelids):

- *Plesictis* (early Oligocene) -- Transitional between miacids (see above) and mustelids (weasels etc.)
- *Potamotherium* (late Oligocene) -- Another early mustelid, but has some rather puzzling traits that may mean it is not a direct ancestor of later mustelids. Mustelids were diversifying with "bewildering variety" by the early Miocene.

Pinniped relationships have been the subject of extensive discussion and analysis. They now appear to be a monophyletic group, probably derived from early bears (or possibly early weasels?).

Seals, sea lions & walruses:

- *Pachycynodon* (early Oligocene) -- A bearlike terrestrial carnivore with several sea-lion traits.
- *Enaliarctos* (late Oligocene, California) -- Still had many features of bear-like terrestrial carnivores: bear-like tympanic bulla, carnassials, etc. But, had flippers instead of toes (though could still walk and run on the flippers) and somewhat simplified dentition. Gave rise to several more advanced families, including:
- Odobenidae: the walrus family. Started with *Neotherium* 14 my, then *Imagotaria*, which is probably ancestral to modern species.
- Otariidae: the sea lion family. First was *Pithanotaria* (mid- Miocene, 11 Ma) -- small and primitive in many respects, then *Thalassoleon* (late Miocene) and finally modern sea lions (Pleistocene, about 2 Ma).
- Phocidae: the seal family. First known are the primitive and somewhat weasel-like mid-Miocene seals *Leptophoca* and *Montherium.* Modern seals first appear in the Pliocene, about 4 Ma.

Now, on to the second major group of carnivores, the cat/civet/hyena line. Civets (viverrids):

- *Stenoplesictis* (early Oligocene) -- An early civet-like animal related to the miacids. Might not be directly ancestral (has some puzzling non-civet-like traits).
- *Palaeoprionodon* (late Oligocene, 30-24 Ma) -- An aeluroid (undifferentiated cat/civet/hyena) with a civet-like skull floor. Probably had split off from the cat line and was on the way to modern viverrids.
- *Herpestides* (early Miocene, 22 Ma, France) -- Had a distinctly civet-like skull floor, more advanced than *Palaeoprionodon.*
- More advanced modern civets appeared in the Miocene.

Cats:

- *Haplogale* (late Oligocene, 30 Ma) -- A slightly cat-like aeluroid (cat/civet/hyena).
- *"Proailurus" julieni*, (early Miocene) -- An aeluroid with a viverrid-ish skull floor that also showed the first cat-like traits. The genus name is in quotes because, though it was first thought to be in *Proailurus*, it's now clear that it was a slightly different genus, probably ancestral to *Proailurus.*
- *Proailurus lemanensis* (early Miocene, 24 Ma) -- Considered the first true cat; had the first really cat-like skull floor, with an ossified bulla.
- *Pseudaelurus* (early-mid Miocene, 20 Ma) -- A slightly later, more advanced cat.
- *Dinictis* (early Oligocene) -- Transitional from early cats such as *Proailurus* to modern "feline" cats
- *Hoplophoneus* (early Oligocene) -- Transitional from early cats to "saber-tooth" cats

Hyaenids:

- Though there are only four species now, hyaenids were once *very* common and have an abundant fossil record. There is a main stem of generally small to medium-sized civet-like forms, showing a general trend toward an increase in size (Werdelin & Solounias, 1991):
- *Herpestes antiquus* (early Miocene) -- A viverrid thought to be the ancestor of the hyenid family.
- *Protictitherium crassum* (& 5 closely related species) (early Miocene, 17-18 Ma) -- Fox-sized, civet-like animals with hyena-like teeth. Transitional between the early civet-like viverrids and all the hyenids. Split into three lines, one of which led to the aardwolf. Another line eventually led to modern hyenas:
- *Plioviverrops orbignyi* (& 3 closely related species)
- *Tungurictis spocki*, a mid-Miocene fox-sized hyenid. Truly hyena-like ear capsule.
- *Ictitherium viverrinum* (& 6 closely related species)
- *Thalassictis robusta* (& 5 other spp.)
- *Hyaenotherium wongii*
- *Miohyaenotherium bessarabicum*
- *Hyaenictitherium hyaenoides* (& 3 other spp.)
- *Palinhyaena reperta*
- *Ikelohyaena abronia*
- *Belbus beaumonti*
- *Leecyaena lycyaenoides* (& 1 other) We're now in the Pliocene.

- *Parahyaena brunnea*
- *Hyaena hyaena*. *Pliocrocuta* (below) split off from *Hyaena* via cladogenesis. *Hyaena* itself continued on mostly unchanged as the modern striped hyena, with one more recent offshoot, the brown hyena,
- *Hyaena brunnea*.
- *Pliocrocuta perrieri*
- *Pachycrocuta brevirostris* (& 1 other)
- *Adcrocuta eximia*, which split into: *Crocuta crocuta* (the modern spotted hyena), *C. sivalensis*, and *C. dietrichi*.

Species-species transitions among carnivores:

- Ginsburg (in Chaline, 1983) describes gradual change in the early cats, from *Haplogale media* to *Proailurus lemansis*, to (in Europe) *Pseudaelurus transitorius* to *Ps. lorteti* to *Ps. rmoieviensis* to *Ps. quadridentatus*. These European lineages gave rise to the modern *Lynx*, *Panthera*, etc. Different lineages of *Pseudaelurus* evolved in North American, Africa, and Asia.
- Hecht (in Chaline, 1983) describes polar bear evolution; the first "polar bear" subspecies, *Ursus maritimus tyrannus*, was a essentially a brown bear subspecies, with brown bear dimensions and brown bear teeth. Over the next 20,000 years, body size reduced and the skull elongated. As late as 10,000 years ago, polar bears still had a high frequency of brown-bear-type molars. Only recently have they developed polar-bear-type teeth.
- Kurten (1976) describes bear transitions: "From the early Ursus minimus of 5 million years ago to the late Pleistocene cave bear, there is a perfectly complete evolutionary sequence without any real gaps. The transition is slow and gradual throughout, and it is quite difficult to say where one species ends and the next begins. Where should we draw the boundary between U. minimus and U. etruscus, or between U. savini and U. spelaeus? The history of the cave bear becomes a demonstration of evolution, not as a hypothesis or theory but as a simple fact of record." He adds, "In this respect the cave bear's history is far from unique."
- Kurten (1968) also described the following known species-species transitions:
  - *Felis issiodorensis* to *Felis pardina* (leopards)
  - *Gulo schlosseri* to *Gulo gulo* (wolverines)
  - *Cuon majori* to *Cuon alpinus* (dholes, a type of short-faced wolf)
- Lundelius et al. (1987) describe a study by Schultz in 1978 that showed an increase in canine length leading from the dirk-tooth cat *Megantereon hesperus* to *Megantereon/Smilodon gracilis*, then to *Smilodon fatalis* (a saber-toothed cat), and then to *Smilodon californicus*. Note the genus transition and the accompanying striking change in morphology.
- Werdelin & Solounias (1991) wrote an extensive monograph on hyenids. They discuss over one hundred (!) named species, with extensive discussion of the eighteen best-known species, and cladistic analysis of *hundreds* of specimens from the *SIXTY-ONE* "reasonably well known" hyaenid fossil species. They concluded:

  > "We view the evolution of hyaenids as overwhelmingly gradual. The species, when studied with regard to their total variability, often grade insensibly into each other, as do the genera. Large specimens of Hyaenotherium wongii are, for example, difficult to distinguish from small specimens of Hyaenictitherium hyaenoides, a distinct genus. Viewed over the entire family, the evolution of hyaenids from small, fox-like forms to large, scavenging, "typical" hyenas can be followed step by step, and the assembly of features defining the most derived forms has taken place piecemeal since the Miocene. Nowhere is there any indication of major breaks identifying macroevolutionary steps."

Rodents

Lagomorphs and rodents are two modern orders that look superficially similar but have long been thought to be unrelated. Until recently, the origins of both groups were a mystery. They popped into the late Paleocene fossil record fully formed -- in North America & Europe, that is. New discoveries of earlier fossils from previously unstudied deposits in *Asia* have finally revealed the probable ancestors of both rodents and lagomorphs -- surprise, they're related after all. (see Chuankuei-Li et al., 1987)

- *Anagale*, *Barunlestes*, or a similar anagalid (mid-late Paleocene) -- A recently discovered order of primitive rodent/lagomorph ancestors from Asia. Rabbit-like lower cheek teeth, with cusps in a pattern that finally explains where the rabbits' central cusp came from (it's the old anagalid protocone). Primitive skeleton not yet specialized for leaping, with unfused leg bones, but has a rabbit-like heel. No gap yet in the teeth. These fossils have just been found in the last decade, and are still being described and analyzed. *Barunlestes* in particular (known so far from just one specimen) has both rodent-like *and* rabbit-like features, and may be ancestral to both the rodents and the lagomorphs. This lineage then apparently split into two groups, a eurymyloid/rodent-like group and a mymotonid/rabbit-like group.

- *Heomys* (mid-late Paleocene, China) -- An early rodent-like eurymyloid. Similar overall to *Barunlestes* but with added rodent/lagomorph features (enamel only on front of incisors, loss of canines and some premolars, long tooth gap) plus various rodent-like facial features and rodent-like cheek teeth. Probably a "cousin" to the rodents, though Chuankuei-Li et al (1987, and in Szalay et al. 1993) think it is "very close to the ancestral stem of the order Rodentia."
- *News flash Tribosphenomys minutus* (late Paleocene, 55 Ma) -- A just-announced discovery; it's a small Asian anagalid known from a single jaw found in some fossilized dung (well, we all have to die somehow). It still had rabbit-like cheek teeth, but had fully rodent-like ever-growing first incisors. This probably *is* the "ancestral stem" of the rodents. (see Discover, Feb. 1995, p. 22).
- *Acritoparamys (was "Paramys") atavus* (late Paleocene) -- First known primitive rodent.
- *Paramys* & its ischyromyid friends (late Paleocene) -- Generalized early rodents; a mostly squirrel-like skeleton but without the arboreal adaptations. Had a primitive jaw musculature (which modern squirrels still retain). Rodent-like gnawing incisors, but cheek teeth still rooted (unlike modern rodents) and primitive rodent dental formula.

Squirrels:

- *Paramys* (see above)
- *Protosciurus* (early Oligocene) An early squirrel with very primitive dentition and jaw muscles, but with the unique ear structure of modern squirrels. Fully arboreal.
- *Sciurus*, the modern squirrel genus. Arose in the Miocene and has not changed since then. Among the rodents, squirrels may be considered "living fossils".

Beavers:

- *Paramys* (see above)
- *Paleocastor* (Oligocene) -- Early beaver. A burrower, not yet aquatic. From here the beaver lineage became increasingly aquatic. Modern beavers appear in the Pleistocene.

Rats/mice/voles:

- *Paramys* (see above)
- Eomyids -- later Eocene rodents with a few tooth and eyesocket features that show they had branched off from the squirrel line.
- Geomyoids -- primitive rodents that have those same tooth & eyesocket features, and still have squirrel-like jaws; Known to have given rise to the mouse family only because we have intermediate fossil forms.
- In the Oligocene these early mice started to split into modern families such as kangaroo rats and pocket gophers. The first really mouse- like rodent, *Antemus*, first appeared in the Miocene (16 Ma) in Asia. In the Plio-Pleistocene, modern mice, hamsters, and voles appeared and started speciating all over the place. Carroll (1988, p. 493) has a nightmarish diagram of vole speciation which I will not try to describe here! The fossil record is very good for these recent rodents, and many examples of species-species transitions are known, very often crossing genus lines (see below).

Cavies:

GAP: No cavy fossils are known between *Paramys* and the late Oligocene, when cavies suddenly appear in modern form in both Africa and South America. However, there are possible cavy ancestors (franimorphs) in the early Oligocene of Texas, from which they could have rafted to South America and Africa. Known species-species transitions in rodents:

- Chaline & Laurin (1986) show gradual change in Plio-Pleistocene water voles, with gradual speciations documented in *every step* in the following lineage: *Mimomys occitanus* to *M. stehlini* to *M. polonicus* to *M. pliocaenicus* to *M. ostramosensis*. The most important change was the development of high-crowned teeth, which allows grass-eating. They say: "The evolution of the lineage appears to involve continuous morphological drift involving functional adaptation processes. It presumably results from changes in diet when Pretiglian steppes were replaced in Europe by a period with forest...In our opinion phyletic gradualism [in this lineage] seems well characterized. It lasts for 1.9 my and leads to very important morphological changes, and the transitional stages in the chronomorphocline are sufficiently easily recognizable that they have been described as morphospecies..."

- In a previous paper, Chaline (1983, p. 83) surveyed speciation in the known arvicolid rodents. About 25% of the species have fossil records complete enough to study the mode of appearance. Of those 25%, a wide variety of modes was seen, ranging sudden appearances (taken to mean punctuated equilibrium), to quick but smooth transitions, to very slow smooth transitions. Both cladogenesis and anagenesis occurred. Overall, smooth species-to-species transitions were seen for 53% of the studied species, but no single mode of evolution was dominant.
- Chevret et al. (1993) describe the transition from mouse teeth to vole teeth (6-4.5 Ma).
- Fahlbusch (1983) documents gradual change in various Miocene rodent transitions.
- Goodwin (in Martin, 1993) describes gradual transitions in prairie dogs, with *Cinomys niobrarius* increasing in size and splitting into two descendants, *C. leucurus* and *C. parvidens*.
- Jaeger (in Chaline, 1983) describes gradual shifts in tooth size and shape two genera of early mice, related to the development of grazing.
- Kurten (1968) describes a transition in voles, from *Lagurus pannonicus* to *L. lagurus*.
- Lundelius et al. (1987) summarizes and reviews species-species transitions in numerous voles, grasshopper mice, jumping mice, etc., from at least 11 different studies. Ex: *Sigmodon medius* to *Sigmodon minor*, and *Zapus sandersi* to *Zapus hudsonius*. The authors point out that some promising, well-fossilized groups have not even been studied yet for species-to-species transitions (e.g. the packrats, *Neotoma*).
- Martin (1993) summarizes and reviews the numerous known Pleistocene rodent species-to-species transitions in muskrats, water voles, grasshopper mice, prairie voles, pocket gophers, and cotton rats. Michaux (in Chaline, 1983) summarized speciations in mice. He found a wide variety of modes of speciation, ranging from sudden appearance to gradual change.
- Rensberger (1981) describes a likely lineage in the development of hypsodonty (high-crowned teeth for eating grass), among seven species of meniscomyine rodents in the genus *Niglarodon*.
- Stuart (1982, described by Barnosky, 1987) showed smooth transitions in water voles, including a genus transition. *Mimomys savini* gradually lost its distinctive tooth characters, including rooted cheek teeth, as it changed into a new genus, *Arvicola cantiana*, which in turn smoothly changed into the modern *A. terrestris*.
- Vianey-Liaud (1972) showed gradual change in two independent lineages of the mid-Oligocene rodent genus *Theridomys*. For example, the molars become gradually more hypsodont over time from species to species.
- Vianey-Liaud & Hartenberger (in Chaline, 1983) also describe gradual shifts in size and shape in Eocene rodents (mainly theridomyids), concluding that gradual evolution explains their data better than punctuated equilibrium.

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[Last Update: March 17, 1997]

Part 2A Contents Part 2C

Lagomorphs

- *Barunlestes* (see above) The possible Asian rodent/lagomorph ancestor.
- *Mimotoma* (Paleocene) -- A rabbit-like animal, similar to *Barunlestes*, but with a *rabbit* dental formula, changes in the facial bones, and only one layer of enamel on the incisors (unlike the rodents). Like rabbits, it had two upper incisors, but the second incisor is still large and functional, while in modern rabbits it is tiny. Chuankuei-Li et al. (1987; also see Szalay et al., 1993) think this is the actual ancestor of *Mimolagus*, next.
- *Mimolagus* (late Eocene) -- Possesses several more lagomorph-like characters, such as a special enamel layer, possible double upper incisors, and large premolars.
- *Lushilagus* (mid-late Eocene) -- First true lagomorph. Teeth very similar to Mimotoma, and modern rabbit & hare teeth could easily have been derived from these teeth.
- After this, the first modern rabbits appeared in the Oligocene.

Known species-to-species transitions in lagomorphs:

- The mid-Tertiary lagomorph *Prolagus* shows a very nice "chronocline" (gradual change over time), grading from one species to the next. Gingerich (1977) says: "In *Prolagus* a very complete fossil record shows a remarkable but continuous and gradual reorganization of the premolar crown morphology in a single lineage."
- Lundelius et al. (1987) mention transitions in Pleistocene rabbits, particularly from *Nekrolagus* to *Sylvilagus*, and from *Pratilepus* to *Aluralagus*. Note that both these transitions cross genus lines. Also see the lagomorph paper in Chaline (1983). Some of these transitions were considered to be "sudden appearances" until the intervening fossils were studied, revealing numerous transitional individuals.

Condylarths, the first hoofed animals

- *Protungulatum* (latest Cretaceous) -- Transitional between earliest placental mammals and the condylarths (primitive, small hoofed animals). These early, simple insectivore- like small mammals had one new development: their cheek teeth had grinding surfaces instead of simple, pointed cusps. They were the first mammal herbivores. All their other features are generalized and primitive -- simple plantigrade five-toed clawed feet, all teeth present (3:1:4:3) with no gaps, all limb bones present and unfused, pointy-faced, narrow small brain, eyesocket not closed.

Within a few million years the condylarths split into several slightly different lineages with slightly different teeth, such as oxyclaenids (the most primitive), triisodontines, and phenacodonts (described in other sections). Those first differences amplified over time as the lineages drifted further and further apart, resulting ultimately in such different animals as whales, anteaters, and horses. It's interesting to see how similar the early condylarth lineages were to each other, in contrast to how different their descendants eventually, slowly, became. Paleontologists believe this is a classic example of how 'higher taxa" such as families and orders arise.

Says Carroll (1988, p.505): "In the case of the cetaceans [whales] and the perissodactyls [horses etc.], their origin among the condylarths has been clearly documented....If, as seems likely, it may eventually be possible to trace the ancestry of most of the placental mammals back to the early Paleocene, or even the latest Cretaceous, the differences between the earliest ancestral forms will be very small -- potentially no more than those that distinguish species or even populations within species. The origin of orders will become synonymous with the origin of species or geographical subspecies. In fact, this pattern is what one would expect from our understanding of evolution going back to Darwin. The selective forces related to the origin of major groups would be seen as no different than those leading to adaptation to very slightly differing enviromments and ways of life. On the basis of a better understanding of the anatomy and relationships of the earliest ungulates, we can see that the origin of the Cetacea and the perissodactyls resulted not from major differences in their anatomy and ways of life but from slight differences in their diet and mode of locomotion, as reflected in the pattern of the tooth cusps and details of the bones of the carpus and tarsus." (p. 505)

Species-to-species transitions among the condylarths:

- The most common fossil mammal from the lower Eocene is a little primitive weasel-looking condylarth called *Hyopsodus*. It was previously known that many very different species of *Hyopsodus* were found at different sites, with (for example) very different tooth size. In 1976, Gingerich analyzed the tooth size of all the known fossils of *Hyopsodus* that could be dated reliably and independently. He found that "the pattern of change in tooth size that emerges is one of continuous gradual change between lineages, with gradual divergence following the separation of new sister lineages." When tooth size is charted against time, it shows the single lineage smoothly splitting into four descendant lineages. (This was one of the first detailed & extensive studies of speciation.)
- By 1985, Gingerich had many more specimens of *Hyopsodus* and of several other Eocene condylarth lineages as well, such as *Haplomylus*. For example: "*Haplomylus speirianus* ...gradually became larger over time, ultimately giving rise to a new species *Haplomylus scottianus*... *Hyopsodus latidens* also became larger and then smaller, ultimately giving rise to a still smaller species, *Hyopsodus simplex*." These analyses were based on *hundreds* of new specimens (505 for *Haplomylus*, and 869 for *Hyposodus*) from Clark's Fork Basin in Wyoming. Note, however, that several other species from the same time showed stasis (particularly *Ectocion*, which was previously reported to show change, but in fact stayed much the same), and that not all species transitions are documented. So transitions are not always found. But sometimes they *are* found.

Cetaceans (whales, dolphins)

Just several years ago, there was still a large gap in the fossil record of the cetaceans. It was thought that they arose from land-dwelling mesonychids that gradually lost their hind legs and became aquatic. Evolutionary theory predicted that they must have gone through a stage where they had were partially aquatic but still had hind legs, but there were no known intermediate fossils. A flurry of recent discoveries from India & Pakistan (the shores of the ancient Tethys Sea) has pretty much filled this gap. There are still no known species-species transitions, and the "chain of genera" is not complete, but we now have a partial lineage, and sure enough, the new whale fossils have legs, exactly as predicted. (for discussions see Berta, 1994; Gingerich et al. 1990; Thewissen et al. 1994; Discover magazine, Jan. 1995; Gould 1994)

- *Eoconodon* or similar triisodontine arctocyonids (early Paleocene) Unspecialized condylarths quite similar to the early oxyclaenid condylarths, but with strong canine teeth (showing first meat-eating tendencies), blunt crushing cheek teeth, and flattened claws instead of nails.
- *Microclaenodon* (mid-Paleocene) -- A transitional genus intermediate between *Eoconodon* and the mesonychids, with molar teeth reorganizing in numerous ways to look like premolars. Adapted more toward carnivory.
- *Dissacus* (mid-Paleocene) -- A mesonychid (rather unspecialized Paleocene meat-eating animal) with molars more like premolars & several other tooth changes. Still had 5 toes in the foot and a primitive plantigrade posture.
- *Hapalodectes* or a very similar mesonychid (early Eocene, around 55 Ma) -- A small mesonychid with very narrow shearing molars, a distinctively shaped zygomatic arch, and peculiar vascularized areas between the molars. Probably a running animal that could swim by paddling its feet. *Hapalodectes* itself may be just too

late to be the whale ancestor, but probably was a close relative of the whale ancestor. Says Carroll (1988): "The skulls of Eocene whales bear unmistakable resemblances to those of primitive terrestrial mammals of the early Cenozoic. Early [whale] genera retain a primitive tooth count with distinct incisors, canines, premolars,, and multirooted molar teeth. Although the snout is elongate, the skull shape resembles that of the mesonychids, especially *Hapalodectes*...."

- *Pakicetus* (early-mid Eocene, 52 Ma) -- The oldest fossil whale known. Same skull features as *Hapalodectes*, still with a very terrestrial ear (tympanic membrane, no protection from pressure changes, no good underwater sound localization), and therefore clearly not a deep diver. Molars still have very mesonychid-like cusps, but other teeth are like those of later whales. Nostrils still at front of head (no blowhole). Whale- like skull crests and elongate jaws. Limbs unknown. Only about 2.5 m long. This skull was found with terrestrial fossils and may have been amphibious, like a hippo.
- *Ambulocetus natans* (early-mid Eocene, 50 Ma) -- A recently discovered early whale, with enough of the limbs and vertebrae preserved to see how the early whales moved on land and in the water. This whale had four legs! Front legs were stubby. Back legs were short but well-developed, with enormous broad feet that stuck out behind like tail flukes. Had no true tail flukes, just a long simple tail. Size of a sea lion. Still had a long snout with no blowhole. Probably walked on land like a sea lion, and swam with a seal/otter method of steering with the front feet and propelling with the hind feet. So, just as predicted, these early whales were much like modern sea lions -- they could swim, but they could also still walk on land. (Thewissen et al., 1994)
- *Rodhocetus* (mid-Eocene, 46 Ma) -- Another very recent (1993) fossil whale discovery. Had hind legs a third smaller than those of *A. natans*. Could probably still "waddle" a bit on land, but by now it had a powerful tail (indicated by massive tail vertebrae) and could probably stay out at sea for long periods of time. Nostrils had moved back a bit from the tip of the snout.
- *Basilosaurus isis*, *Protocetes*, *Indocetus ramani* and similar small-legged whales of the mid-late Eocene (45-42 Ma) -- After *Rodhocetus* came several whales that still had hind legs, but couldn't walk on them any more. For example, *B. isis* (42 Ma) had hind feet with 3 toes and a tiny remnant of the 2nd toe (the big toe is totally missing). The legs were small and must have been useless for locomotion, but were specialized for swinging forward into a locked straddle position -- probably an aid to copulation for this long-bodied, serpentine whale. *B. isis* may have been a "cousin" to modern whales, not directly ancestral. Another recent discovery is *Protocetes*, a slightly more advanced whale from the late Eocene. It was about 3m long (dolphin sized), and still had primitive dentition, nostrils at end of snout, and a large pelvis attached to the spine; limbs unknown. Finally *Indocetus* is known from only fragmentary remains, but these include a tibia. These late Eocene legged whales still had mesonychid-like teeth, and in fact, some of the whale fossils were first mis-identified as mesonychids when only the teeth were found. (See Gingerich et al. (1990) for more info on *B. isis*.)
- *Prozeuglodon* (late Eocene, 40 Ma) Another recently discovered whale, found in 1989. Had *almost* lost the hind legs, but not quite: still carried a pair of vestigial 6- inch hind legs on its 15-foot body.
- *Eocetus*, & similar "archeocete whales" of the late Eocene These more advanced whales have lost their hind legs entirely, but retain a"primitive whale" skull and teeth, with unfused nostrils. They grew to larger body size (up to 25m by the end of the Eocene), an had an elongate, streamlined body, flippers, and a cartilaginous tail fluke. The ear was modified for hearing underwater. Note that this stage of aquatic adaptation was attained about 15 million years after the first terrestrial mesonychids.
- *Dorudon intermedius* -- a late Eocene whale probably ancestral to modern whales.

In the Oligocene, whales split into two lineages:

1. Toothed whales:
    - *Agorophius* (late Oligocene) -- Skull partly telescoped, but cheek teeth still rooted. Intermediate in many ways between archaeocetes and later toothed whales.
    - *Prosqualodon* (late Oligocene) -- Skull fully telescoped with nostrils on top (blowhole). Cheek teeth increased in number but still have old cusps. Probably ancestral to most later toothed whales (possibly excepting the sperm whales?)
    - *Kentriodon* (mid-Miocene) -- Skull telescoped, still symmetrical. Radiated in the late Miocene into the modern dolphins and small toothed whales with asymmetrical skulls.
2. Baleen (toothless) whales:
    - *Aetiocetus* (late Oligocene) -- The most primitive known mysticete whale and probably the stem group of all later baleen whales. Had developed mysticete-style loose jaw hinge and air sinus, *but*

still had all its teeth. Later,
  - *Mesocetus* (mid-Miocene) lost its teeth.
  - Modern baleen whales first appeared in the late Miocene.

Perissodactyls (horses, tapirs, rhinos)

Here we come to the most famous general lineage of all, the horse sequence. It was the first such lineage to be discovered, in the late 1800's, and thus became the most famous. There is an odd rumor circulating in creationist circles that the horse sequence is somehow suspect or outdated. Not so; it's a very good sequence that has grown only more detailed and complete over the years, changing mainly by the addition of large side-branches. As these various paleontologists have said recently: "The extensive fossil record of the family Equidae provides an excellent example of long-term, large-scale evolutionary change." (Colbert, 1988) "The fossil record [of horses] provides a lucid story of descent with change for nearly 50 million years, and we know much about the ancestors of modern horses."(Evander, in Prothero & Schoch 1989, p. 125) "All the morphological changes in the history of the Equidae can be accounted for by the neo-Darwinian theory of microevolution: genetic variation, natural selection, genetic drift, and speciation." (Futuyma, 1986, p.409) "...fossil horses do indeed provide compelling evidence in support of evolutionary theory." (MacFadden, 1988)

So here's the summary of the horse sequence. For more info, see the Horse Evolution FAQ.

- *Loxolophus* (early Paleocene) -- A primitive condylarth with rather low-crowned molars, probably ancestral to the phenacodontid condylarths.
- *Tetraclaenodon* (mid-Paleocene) -- A more advanced Paleocene condylarth from the phenacodontid family, and almost certainly ancestral to all the perissodactyls (a different order). Long but unspecialized limbs; 5 toes on each foot (#1 and #5 smaller). Slightly more efficient wrist.

GAP: There are almost no known perissodactyl fossils from the late Paleocene. This is actually a small gap; it's only noticeable because the perissodactyl record is otherwise very complete. Recent discoveries have made clear that the first perissodactyls arose in Asia (a poorly studied continent), so hopefully the ongoing new fossil hunts in Asia will fill this small but frustrating gap. The first clue has already come in:

- *Radinskya yupingae* (late Paleocene, China) -- A recently discovered perissodactyl-like condylarth. (McKenna et al., in Prothero & Schoch, 1989.)
- *Hyracotherium* (early Eocene, about 55 Ma; previously "Eohippus") -- The famous "dawn horse", a small, doggish perissodactyl, with an arched back, short neck, omnivore teeth, and short snout. 4 toes in front and 3 behind. Compared to *Tetraclaenodon*, has longer toes, interlocking ankle bones, and slightly different tooth cusps. Probably evolved from *Tetra.* in about 4-5 my, perhaps via an Asian species like *Radinskya*. Note that *Hyrac.* differed from other early perissodactyls (such as tapir/rhino ancestors) only by small changes in tooth cusps and in body size.
- *Hyracotherium vassacciense* (early Eocene) -- The particular species that probably gave rise to the equids.
- *Orohippus* (mid-Eocene, ~50 Ma) -- Small, 4/3 toed, developing browser tooth crests.
- *Epihippus* (late Eocene, ~45 Ma) -- Small, 4/3 toed, good tooth crests, browser.
- *Epihippus (Duchesnehippus)* -- A later subgenus with *Mesohippus*-like teeth.
- *Mesohippus celer* (latest Eocene, 40 Ma) -- Three-toed on all feet, browser, slightly larger
- *Mesohippus westoni* (early Oligocene) -- A slightly later, more advanced species.
- *Miohippus assiniboiensis* (mid-Oligocene) -- This species split off from early *Mesohippus* via cladogenetic evolution, after which *Miohippus* and *Mesohippus* overlapped for the next 4 my. Distinctly larger, slightly longer skull, facial fossa deeper and more expanded, subtly different ankle joint, variable extra crest on upper cheek teeth. In the early Miocene (24 My) Miohippus began to speciate rapidly. Grasses had just evolved, & teeth began to change accordingly. Legs, etc., started to change for fast running.
- *Kalobatippus* (late Oligocene) -- Three-toed browser w/foot intermediate between Mio. & Para.
- *Parahippus* (early Miocene, 23 Ma) -- Three-toed browser/grazer, developing "spring foot". Permanent establishment of the extra crest that was so variable in Miohippus. Stronger tooth crests & slightly taller tooth crowns.
- *'Parahippus' leonensis* (mid-Miocene, ~20 Ma) -- Three-toed browser/grazer with the emphasis on grazer. Developing spring-foot & high-crowned teeth.

- *'Merychippus' gunteri* (mid-Miocene, ~18 Ma) -- Three-toed grazer, fully spring-footed with high-crowned teeth.
- *Merychippus primus* (mid-Miocene, ~17 Ma) -- Slightly more advanced.
- *Merychippus* spp. of mid-late Miocene (16-15 Ma) -- 3-toed grazers, spring-footed, size of small pony. Diversified into all available grazer niches, giving rise to at least 19 successful three-toed grazers. Side toes of varying sizes, very small in some lines. Horsey hoof develops, leg bones fuse. Fully high-crowned teeth with thick cement & same crests as Parahippus. The line that eventually produced *Equus* developed as follows: M. primus, M. sejunctus, M. isonesus (these last two still had a mix of primitive, hipparion, and equine features), M. intermontanus, M. stylodontus, M. carrizoensis. These last two looked quite horsey, with quite small side toes, and gave rise to a set of larger three-toed and one-toed horses known as the "true equines". Crystal clear, right?

SMALL GAP: It is not known which Merychippus species (stylodontus? carrizoensis?) gave rise to the first Dinohippus species (Evander, in Prothero & S 1988).

- *Dinohippus* (late Miocene, 12 Ma) -- *One*-toed grazer, spring-footed. Very equine feet, teeth, and skull, with straighter teeth & smaller fossae. First was D. spectans, followed by D. interpolatus and D. leidyanus. A slightly later species was D. mexicanus, with even straighter teeth and even smaller fossae.
- *Equus (Plesippus)*, also called the "*E. simplicidens*" group (Pliocene, ~4 My) -- Three closely related species of one-toed spring-footed high-crowned grazers. No fossae and very straight teeth. Pony size, fully "horsey" body -- rigid spine, long neck, long legs, fused leg bones with no rotation, long nose, flexible muzzle, deep jaw. The brain was a bit larger than in early Dinohippus. Still had some primitive traits such as simple teeth & slight facial fossae, which later Equus species lost. These "simple Equus" species quickly diversified into at least 12 new species in 4 different groups. During the first major glaciations of the late Pliocene (2.6 Ma), certain *Equus* species crossed to the Old World. Worldwide, Equus took over the niche of "large coarse-grazing plains runner".
- *Equus (Hippotigris)* (Pleistocene) -- Subgenus of modern 1-toed spring-footed grazing zebras.
- *Equus (Equus)* (Pleistocene) -- Subgenus of modern 1-toed spring-footed grazing horses & donkeys. [note: very rarely a horse is born with small side toes, indicating that some horses retain the genes for side toes.]

Compare *Equus* to *Hyracotherium* and see how much it has changed. If you think of animals as being divided into "kinds", do you think Equus and Hyracotherium can be considered the same "kind"? Tapirs and rhinos:

- *Loxolophus*, see above
- *Tetraclaenodon*, see above
- *Homagalax* (early Eocene) -- Very like its sister genus *Hyracotherium*, but had cross-lophs on teeth. Note that these early perissodactyls differed only in slight details of the teeth.
- *Heptodon* (late early Eocene) -- A small early tapiroid showing one more tooth cusp change. Split into two lineages:
    1. *Helaletes* (mid-Eocene) which had a short proboscis, then *Prototapir* (late Oligocene), much like modern tapirs but without such a flexible snout, then *Miotapirus* (early Miocene), an almost- modern tapir with a flexible snout, then *Tapirus* (Pliocene) the modern tapir.
    2. *Hyrachyus* (late Eocene), a tapiroid with increased shearing function in its teeth. Led to the late Eocene hyracodontids such as *Hyracodon* (rhino-tapiroids, or "running rhinos") that show increasing development of high-crowned teeth and larger body size. They led to *Caenopus* (early Oligocene), a large, hornless, generalized rhino which led to the modern horned rhinos of the Miocene & Pliocene. Our living genera first appear in the Pliocene, about 4 Ma.

Species-species transitions:

- Horses: Gingerich (1980) documented speciation from *Hyracotherium grangeri* to *H. aemulor*. Prothero & Schoch (1989) mention some intermediate fossils that link late *Orohippus* to *Mesohippus celer*. MacFadden (1985) has documented numerous smooth transitions among the three-toed horses, particularly among *Merychippus* and the various hipparions. Hulbert (in Prothero & Schoch, 1989) showed that *Dinohippus* smoothly grades into *Equus* through successive Pliocene strata. Simpson (1961) describes gradual loss of the side toes in *Pliohippus* through 3 successive strata of the early Pliocene.
- Rhinos: Wood (1954) said of the rhino fossils "whenever we do have positive paleontological evidence, the picture is of the most extreme gradualism" (quoted in Gingerich, 1977), and Kurten (1968) describes a smooth transition between *Dicerorhinus* species.

Elephants

- *Minchenella* or a similar condylarth (late Paleocene) -- Known only from lower jaws. Has a distinctive broadened shelf on the third molar. The most plausible ancestor of the embrithopods & anthracobunids.
- *Phenacolophus* (late Paleocene or early Eocene) -- An early embrithopod (very early, slightly elephant-like condylarths), thought to be the stem-group of all elephants.
- *Pilgrimella* (early Eocene) -- An anthracobunid (early proto-elephant condylarth), with massive molar cusps aligned in two transverse ridges.
- Unnamed species of proto-elephant (early Eocene) -- Discovered recently in Algeria. Had slightly enlarged upper incisors (the beginnings of tusks), and various tooth reductions. Still had "normal" molars instead of the strange multi-layered molars of modern elephants. Had the high forehead and pneumatized skull bones of later elephants, and was clearly a heavy-boned, slow animal. Only one meter tall.
- *Moeritherium*, *Numidotherium*, *Barytherium* (early-mid Eocene) -- A group of three similar very early elephants. It is unclear which of the three came first. Pig-sized with stout legs, broad spreading feet and flat hooves. Elephantish face with the eye set far forward & a very deep jaw. Second incisors enlarged into short tusks, in upper *and* lower jaws; little first incisors still present; loss of some teeth. No trunk.
- *Paleomastodon*, *Phiomia* (early Oligocene) -- The first "mastodonts", a medium-sized animals with a trunk, long lower jaws, and short upper and lower tusks. Lost first incisors and canines. Molars still have heavy rounded cusps, with enamel bands becoming irregular. *Phiomia* was up to eight feet tall.

GAP: Here's that Oligocene gap again. No elephant fossils at all for several million years.

- *Gomphotherium* (early Miocene) -- Basically a large edition of *Phiomia*, with tooth enamel bands becoming very irregular. Two long rows cusps on teeth became cross- crests when worn down. Gave rise to several families of elephant- relatives that spread all over the world. From here on the elephant lineages are known to the species level.
- The mastodon lineage split off here, becoming more adapted to a forest browser niche, and going through *Miomastodon* (Miocene) and *Pliomastodon* (Pliocene), to *Mastodon* (or "Mammut", Pleistocene).

Meanwhile, the elephant lineage became still larger, adapting to a savannah/steppe grazer niche:

- *Stegotetrabelodon* (late Miocene) -- One of the first of the "true" elephants, but still had two long rows of cross-crests, functional premolars, and lower tusks. Other early Miocene genera show compression of the molar cusps into plates (a modern feature), with exactly as many plates as there were cusps. Molars start erupting from front to back, actually moving forward in the jaw throughout life.
- *Primelephas* (latest Miocene) -- Short lower jaw makes it look like an elephant now. Reduction & loss of premolars. Very numerous plates on the molars, now; we're now at the modern elephants' bizarre system of one enormous multi-layered molar being functional at a time, moving forward in the jaw.
- *Primelephas gomphotheroides* (mid-Pliocene) -- A later species that split into three lineages, Loxodonta, Elephas, and Mammuthus:
    1. *Loxodonta adaurora* (5 Ma). Gave rise to the modern African elephant *Loxodonta africana* about 3.5 Ma.
    2. *Elephas ekorensis* (5 Ma), an early Asian elephant with rather primitive molars, clearly derived directly from *P. gomphotheroides*. Led directly to:
        - *Elephas recki*, which sent off one side branch, *E. hydrusicus*, at 3.8 Ma, and then continued changing on its own until it became *E. iolensis*.
        - *Elephas maximus*, the modern Asian elephant, clearly derived from
        - *E. hysudricus*. Strikingly similar to young *E. hysudricus* animals. Possibly a case of neoteny (in which "new" traits are simply juvenile features retained into adulthood).
    3. *Mammuthus meridionalis*, clearly derived from *P. gomphotheroides*. Spread around the northern hemisphere. In Europe, led to *M. armeniacus/trogontherii*, and then to *M. primigenius*. In North America, led to *M. imperator* and then *M. columbi*.

The Pleistocene record for elephants is very good. In general, after the earliest forms of the three modern genera appeared, they show very smooth, continuous evolution with almost half of the speciation events preserved in fossils. For instance, Carroll (1988) says: "Within the genus *Elephas*, species demonstrate continuous change over a period of 4.5 million years. ...the elephants provide excellent evidence of significant morphological change within species, through species within genera, and through genera within a family...."

Species-species transitions among the elephants:

- Maglio (1973) studied Pleistocene elephants closely. Overall, Maglio showed that at least 7 of the 17 Quaternary elephant species arose through smooth anagenesis transitions from their ancestors. For example, he said that *Elephas recki* "can be traced through a progressive series of stages...These stages pass almost imperceptibly into each other....In the late Pleistocene a more progressive elephant appears which I retain as a distinct species, *E. iolensis*, only as a matter of convenience. Although as a group, material referred to *E. iolensis* is distinct from that of *E. recki*, some intermediate specimens are known, and *E. iolensis* seems to represent a very progressive, terminal stage in the *E. recki* specific lineage."
- Maglio also documented very smooth transitions between three Eurasian mammoth species: *Mammuthus meridionalis* --> *M. armeniacus* (or *M. trogontherii*) --> *M. primigenius*.
- Lister (1993) reanalyzed mammoth teeth and confirmed Maglio's scheme of gradual evolution in European mammoths, and found evidence for gradual transitions in the North American mammoths too.

Sirenians (dugongs & manatees)

GAP: The ancestors of sirenians are not known. No sirenian-like fossils are known from before the Eocene.

- Early Eocene -- fragmentary sirenian fossils known from Hungary.
- *Prorastomus* (mid-Eocene) -- A very primitive sirenian with an extremely primitive dental formula (including the ancient fifth premolar that all other mammals lost in the Cretaceous! Could this mean sirenians split off from all other mammals very early on?) The skull is somewhat condylarth-like. Had distinctive sirenian ribs. Not enough of the rest of the skeleton was found to know how aquatic it was.
- *Protosiren* (late Eocene) -- A sirenian with an essentially modern skeleton, though it still had the very primitive dental formula. Probably split into the two surviving lineages:
    1. Dugongs: *Eotheroides* (late Eocene), with a slightly curved snout and small tusks, still with the primitive dental formula. Perhaps gave rise to *Halitherium* (Oligocene) a dugong-ish sirenian with a more curved snout and longer tusks, and then to living dugongs, very curved snout & big tusks.
    2. Manatees: *Sirenotherium* (early Miocene); *Potamosiren* (late Miocene), a manatee-like sirenian with loss of some cheek teeth; then *Ribodon* (early Pliocene), a manatee with continuous tooth replacement, and then the living manatees.

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Transitional Vertebrate Fossils FAQ
Part 2C

[Last Update: March 17, 1997]

Part 2B Contents

Artiodactyls (cloven-hoofed animals)

"The early evolution of the artiodactyls is fairly well documented by both the dentition and the skeletal material and provides the basis for fairly detailed analysis of evolutionary patterns....the origin of nearly all the recognized families can be traced to the late Middle Eocene or the Upper Eocene..." (Carroll, 1988)

- *Chriacus* (early Paleocene) -- A primitive oxyclaenid condylarth from the Lower Paleocene. Has many tooth features linking it to later *Diacodexis*; but in all other ways, including the legs, it was an unspecialized condylarth.

GAP: No artiodactyl fossils known from the late Paleocene. Similar late Paleocene gaps in rodents, lagomorphs, and perissodactyls are currently being filled with newly discovered Asian fossils, so apparently much late Paleocene herbivore evolution occurred in central Asia. Perhaps the new Asian expeditions will find Paleocene artiodactyl fossils too. At any rate, somewhere between Chriacus & Diacodexis, the hind leg changed, particularly the ankle, to allow smooth running.

- *Diacodexis* (early Eocene) -- A rabbit-sized with longer limbs than the condylarths. The fibula was reduced to a splint, and in some (but not all!) individuals, fused partially to the tibia. Artiodactyl-like "double pulley" ankle (because of this feature, *Diacodexis* is automatically classified as the first artiodactyl). The feet were very elongated, and the 3rd and 4th toes bore the most weight. Many primitive, non-artiodactyl features retained: collarbone, unfused ulna, primitive femur, unfused foot bones with all 5 toes, could still spread hind limb out to the side, very primitive skull & teeth (all teeth present, no gaps, simple cusps). In fact, in most ways, Diacodexis is just a leggy condylarth. Only the ankle shows that it was in fact the ancestor of all our modern cloven-hoofed animals (possible exception: the hippos & pigs may have split off earlier). There are abundant species-to- species transitions linking *Diacodexis* to various artiodactyl familes (see below).

Hippos & pigs:

- *Helohyus* or a similar helohyid (mid-Eocene) -- Primitive artiodactyl, larger than *Diacodexis* but with relatively shorter & stouter limbs, with bulbous cusps on the molars.
- *Anthracotherium* and later anthracotheriids (late Eocene) -- A group of heavy artiodactyls that started out dog-size and increased to be hippo-size. Later species became amphibious with hippo-like teeth. Led to the modern hippos in the early Miocene, 18 Ma.
- *Propalaeochoerus* or a similar cebochoerid/choeropotamid (late Eocene) -- Primitive piglike artiodactyls derived from the helohyids (see above).
- *Perchoerus* (early Oligocene) -- The first known peccary.
- *Paleochoerus* (early Oligocene, 38 Ma) -- First known true pig, apparently ancestral to all modern pigs. Pigs on the whole are still rather primitive artiodactyls; they lost the first toe on the forefoot and have long

curving canines, but have very few other skeletal changes and still have low-cusped teeth. The main changes are a great lengthening of the skull & development of curving side tusks. These changes are seen *Hyotherium* (early Miocene), probably ancestral to the modern pig *Sus* and other genera.

Camels:

- *Diacodexis* (early Eocene, see above)
- *Homacodon* & other dichobunids (mid-Eocene) -- Similar to Diacodexis but with some advances; probably close to the ancestry of the rest of the artiodactyls.
- *Poebrodon* (late Eocene) -- First primitive camelid. Like other late Eocene artiodactyls, it had developed crescent-shaped grinding ridges on the cheek teeth. A small, short-necked, four-toed animal with little hooves on each toe.
- *Poebrotherium* (mid-Oligocene) -- A taller camelid with fused arm & leg bones, and missing toes 1, 4, and 5. Longer neck, though still much shorter than modern camels. Had hooves.
- From here the camel lineage developed pads in place of hooves on the feet, reverted to digitigrade posture, and began pacing instead of trotting, as shown by Miocene fossil footprints. This camel lineage goes through *Protomeryx* (early Miocene) and *Procamelus* (Miocene). The llamas split off here (*Lama*). The main camel lineage continued through *Pliauchenia* (Pliocene) and finally, in the late Pliocene, *Camelus*, the modern camels.

Ruminants: (see Scott & Janis, in Szalay et al., 1993, for details)

It's been very difficult to untangle the phylogeny of this fantastically huge, diverse, and successful group of herbivores. From the Eocene on, there are dozens of similar species, only some of them leading to modern lineages, with others in dozens of varied offshoot groups. Only recently have the main outlines become clear. The phylogeny listed below will probably change a bit as new information comes in.

- *Diacodexis* (early Eocene, see above)
- *Homacodon* & other dichobunids (mid-Eocene, see above)
- *Mesomeryx* (late Eocene) -- A more advanced dichobunid; probably close to the ancestry of the rest of the artiodactyls.
- *Hypertragulus*, *Indomeryx* or a similar hypertragulid (late Eocene) -- Primitive ruminants with a tendency toward crescent ridges on teeth, high-crowned teeth, and loss of one cusp on the upper molars. Long- legged runners and bounders, with many primitive features, but with telltale transitional signs: Still 5 toes on front and 4 behind, but the side toes are now smaller. Fibula still present (primitive), but now partially fused at the ends with the tibia. Upper incisors still present, but now smaller. Upper canine still pointed, but now the lower canine is like an incisor. Ulna and radius fused (new feature). Postorbital bar incomplete (primitive feature). Two ankle bones fused (new feature). Mastoid bone exposed on the surface of the skull (primitive feature).
- *Hyemoschus* or other tragulids (Oligocene) -- Slightly more advanced ruminants called "tragulids" that have the above features plus loss of part of the first toe, some more bones fused, fibula shaft no longer ossifies. Too late to be actual ancestors; probably "cousins". Some later tragulids are still alive and are considered the most primitive living ruminants.
- *Archaeomeryx*, *Leptomeryx* (mid-late Eocene) -- Rabbit-sized ruminants. Still had small upper incisors. The mastoid bone becomes less and less exposed in these "leptomerycids".
- *Bachitherium* (early Oligocene) -- A later, more advanced leptomerycid.
- *Lophiomeryx*, *Gelocus* (late Eocene, early Oligocene) -- The most advanced ruminants yet, called "gelocids", with a more compact and efficient ankle, still smaller side toes, more complex premolars and an almost completely covered mastoid bone. A slightly different lineage split off from this gelocid family in the late Eocene or early Oligocene, eventually giving rise to these four families:
    1. Deer: *Prodremotherium* (late Eocene), a slightly deerlike ruminant, and *Eumeryx* (Oligocene), a more deer-like ruminant, *Dicrocerus* (early Miocene), with the first antlers (similar to living muntjacs), *Acteocemas* (Miocene), and then a shmoo of successful Miocene & Pliocene groups that survive today as modern deer -- cervines, white- tails, moose, reindeer, etc.
    2. Giraffes: Branched off from the deer just after *Eumeryx*. The first giraffids were *Climacoceras* (very earliest Miocene) and then *Canthumeryx* (also very early Miocene), then *Paleomeryx* (early Miocene), then *Palaeotragus* (early Miocene) a short-necked giraffid complete with short skin-covered horns. From here the giraffe lineage goes through *Samotherium* (late Miocene), another

short-necked giraffe, and then split into *Okapia* (one species is still alive, the okapi, essentially a living Miocene short-necked giraffe), and *Giraffa* (Pliocene), the modern long-necked giraffe.

3. Pronghorns: *Paracosoryx prodromus* (early Miocene, 21 Ma) a primitive antilocaprid, probably derived from a North American branch of the bovid lineage. Next came *Merycodus* (Miocene), with branched permanent horns. Led to numerous antilocaprids in the Pliocene. Only the pronghorn is still alive.
4. Bovids: known from isolated teeth in the late Oligocene, then from *Eotragus*, a primitive ancestral mid-Miocene bovid. *Protragocerus* (Miocene) soon followed. The first sheep (*Oioceros*) and gazelles (*Gazella*) are known from the mid-late Miocene (14 Ma), the first cattle (*Leptobos*, *Parabos*) from the early Pliocene (5 Ma).

Species-species transitions in artiodactyls:

- Brunet & Heintz (1983) describe gradual shifts in size and shape in Plio-Pleistocene artiodactyls (cited in Gingerich, 1985)
- Harris & White (1979) show smooth species-species transitions among pigs.
- Krishtalka & Stucky (1985) documented smooth transitions in the common early Eocene artiodactyl genus *Diacodexis*. The fossil record for these animals is very good (literally hundreds of new specimens have been found in Colorado and Wyoming since the 1970's). Analysis of these specimens found gradual species-species transitions for *every step* of the following lineage, including the origination of *three* different familes: *Diacodexis secans-primus* is the first artiodactyl species known. Immediately a new group of animals split off that gave rise to the *Wasatchia* and *Bunophorus* genera (not further discussed by this particular paper). Meanwhile, the main lineage of *D. s-primus* continued, and became *D. s-metsiacus*. Two species split off from *D. s-metsiacus*: one was *D. gracilis*, the other was an as-yet-unnamed new species "Artiodactyla A", which gave rise to "Artiodactyla B"; these two were the first members of the new families Homacodontidae and Antiacodontidae. Meanwhile, *D. s- metsiacus* continued changing and became *D. s-kelleyi*. Another species forked off, *D. minutus*. Slightly later another species forked off, *D. woltonensis*, which apparently was the first member of the new family Leptochoeridae. Meanwhile, *D. s-kelley* continued changing and became *D. s-secans*. Some quotes from the paper: "A good fossil record, such as that of *Diacodexis*, flies major anagenetic change in the face of artificial [naming] conventions..." "Evolutionary change (both anagenesis and cladogenesis) among these artiodactyls appears to have been gradual, chronoclinal, and mosaic, involving an increase in the degree of expression and frequency of occurrence of derived morphologic features..." "...it appears that different taxa of artiodactyls -- in hindsight, the most primitive members of originating suborders, families, and subfamilies -- arose at different times from different lineage segments of the single species *Diacodexis secans*." The authors conclude: "Microevolutionary processes can account for both cladogenetic and anagenetic change among these artiodactyls; macroevolutionary processes are not called for."
- Kurten (1968) describes a transition between *Dama clactonia* to *Dama dama* (deer)
- Lister (in Martin, 1993) describes transitional moose antlers linking a Pleistocene moose, *Alces latifrons*, to the modern moose, *Alces alces*.
- Wilson (1971) describes the gradual evolution of the late middle Eocene *Protoreodon* (family Agriochoeridae), showing progressive development of crescentic tooth cusps & other significant dental features. The species split into two diverging lineages which smoothly led to 1) *Agriochoerus* and 2) the oreodon *Merycoidodon*, which was the first member of a new, different, and eventually very successful family, *Merycoidodontidae*.
- Vrba (in Chaline, 1983) studied speciation in the wildebeest tribe (specialist grazers) and the impala tribe (generalist browsers). She saw almost no smooth transitions among the numerous and diverse wildebeest/blesbuck/etc. species, and concluded that they have arisen mostly by punctuated equilibrium by "fortuitous subdivision of gene pools" due to repeated oscillations in African climate, rainfall & vegetation). The impalas, in contrast, have evolved smoothly in a single non-splitting lineage since the Miocene.

Species-species transitions known from other misc. mammal groups

- Bookstein et al. (1975) describef gradual shifts in mean size in early Eocene mammals (cited in Gingerich, 1985).

- Gingerich (1980) documented gradual change in a lineage of early Eocene tillodonts: *Esthonyx xenicus* to *E. oncylion* to *E. grangeri*.
- Hulbert and Morgan (in Martin, 1993) describe gradual evolution through 2.3 million years in a genus of giant armadillo in Florida, *Holmesina*, with a noticeable spurt of evolution at 1.1 Ma when *H. septentrionalis* changed to *H. floridanus*.

This concludes our tour of the Cenozoic placental mammal record! However, please do not unfasten your seatbelts until the FAQ has come to a complete stop.

A quote from Gingerich (1985) about Eocene mammals also applies to the mammal record as a whole: "The fossil record of early Eocene mammals appears to be both gradual and punctuated. It is gradual in the sense that early and late representatives of all species, whether changing or not, are connected by intermediate forms. Some ancestor-descendant pairs of species are also connected by intermediates. The record is punctuated in the sense that new lineages appear abruptly at the Clarkforkian-Wasatchian boundary, and some possible ancestor-descendant pairs of species are not connected by intermediates."

In summary, as Carroll (1988) said, "There is considerable evidence from Tertiary mammals that significant change does occur during the duration of species, as they are typically recognized, and this change can account for the emergence of new species and genera."

Conclusion: What does the vertebrate fossil record show?

I've tried to present a reasonably complete picture of the vertebrate record as it is now known. As extensive as it may seem, this is still just a crude summary, and I had to leave out some very large groups. For instance, notice that this list mostly includes transitional fossils that happened to lead to modern, familiar animals. This may unintentionally give the impression that fossil lineages proceed in a "straight line" from one fossil to the next. That's not so; generally at any one time there are a whole raft of successful species, only a few of which happened to leave modern descendents. The horse family is a good example; *Merychippus* gave rise to something like 19 new three-toed grazing horse species, which traveled all over the Old and New Worlds and were very successful at the time. Only one of these lines happened to lead to *Equus*, though, so that's the only line I described. As they say, "Evolution is not a ladder, it's a branching bush."

A Bit Of Historical Background

When *The Origin Of Species* was first published, the fossil record was poorly known. At that time, the complaint about the lack of transitional fossils bridging the major vertebrate taxa was perfectly reasonable. Opponents of Darwin's theory of common descent (the theory that evolution has occurred; not to be confused with the separate theory that evolution occurs *specifically* by natural selection) were justifiably skeptical of such ideas as birds being related to reptiles. The discovery of *Archeopteryx* only two years after the publication of *The Origin of Species* was seen a stunning triumph for Darwin's theory of common descent. *Archeopteryx* has been called the single most important natural history specimen ever found, "comparable to the Rosetta Stone" (Alan Feduccia, in "The Age Of Birds"). O.C. Marsh's groundbreaking study of the evolution of horses was another dramatic example of transitional fossils, this time demonstrating a whole sequence of transitions within a single family. Within a few decades after the *Origin*, these and other fossils, along with many other sources of evidence (such as developmental biology and biogeography) had convinced the majority of educated people that evolution *had* occurred, and that organisms *are* related to each other by common descent.

Since then, *many* more transitional fossils have been found, as sketched out in this FAQ. Typically, the only people who still demand to see transitional fossils are either unaware of the currently known fossil record (often due to the shoddy and very dated arguments presented in current creationist articles) or are unwilling to believe it for some reason.

What Does The Fossil Record Show Us Now?

I think the most noticeable aspects of the vertebrate fossil record, those which must be explained by any good model of the development of life on earth, are:

1. A remarkable temporal pattern of fossil morphology, with "an obvious tendency for successively higher and more recent fossil assemblages to resemble modern floras and faunas ever more closely" (Gingerich, 1985) and with animal groups appearing in a certain unmistakable order. For example, primitive fish appear first,

amphibians later, then reptiles, then primitive mammals, then (for example) legged whales, then legless whales. This temporal- morphological correlation is *very* striking, and appears to point overwhelmingly toward an origin of all vertebrates from a common ancestor.

2. Numerous "chains of genera" that appear to link early, primitive genera with much more recent, radically different genera (e.g. reptile- mammal transition, hyenids, horses, elephants), and through which major morphological changes can be traced. Even for the spottiest gaps, there are a few isolated intermediates that show how two apparently very different groups could, in fact, be related to each other (ex. *Archeopteryx*, linking reptiles to birds).
3. Many known species-to-species transitions (primarily known for the relatively recent Cenozoic mammals), often crossing genus lines and occasionally family lines, and often resulting in substantial adaptive changes.
4. A large number of gaps. This is perhaps the aspect that is easiest to explain, since for stratigraphic reasons alone there must always be gaps. In fact, *no* current evolutionary model predicts or requires a complete fossil record, and *no one* expects that the fossil record will ever be even close to complete. As a rule of thumb, however, creationists think the gaps show fundamental biological discontinuities, while evolutionary biologists think they are the inevitable result of chance fossilizations, chance discoveries, and immigration events.

Good Models, Bad Models (or, "The FAQ author rambles on for a while")

And now we come to the main question. Which of the many theories of the origins of life on earth are consistent with the known vertebrate fossil record, and explain its major features? I'll go back to the two main models I outlined at the beginning, creationism and evolution, and break them down further into several different possibilities. I'll try to summarize what they say, and whether or not they are consistent with the major features of the fossil record.

1. Evolution alone (with no God, *or* with a non-interfering God)

   Evolution of all vertebrates by descent from a common ancestor, with change occurring both through punctuated equilibrium and gradual evolution, and with both modes of species formation (anagenesis and cladogenesis). These mechanisms and modes are consistent with (and in fact are predicted by) what is presently known about mutation, developmental biology, and population genetics According to this model, the remaining gaps in the fossil record are primarily due to the chance events of fossilization (particularly significant if evolution occurs locally or rapidly), in combination with immigration (the spreading of a new species from the site where it evolved out into different areas).
2. Evolution with a "Starting-gate God"

   Evolution by common descent, as above, with God having set everything in motion in the beginning -- for instance, at the initial creation of the universe, or at the initial occurrence of life on earth -- and not having affected anything since.
3. Evolution with a "Tinkering God"

   Evolution by common descent, as above, with God occasionally altering the direction of evolution (e.g., causing sudden extinctions of certain groups, causing certain mutations to arise). The extent of the "tinkering" could vary from almost none to constant adjustments. However, a "constant tinkering" theory may run into the problem that vertebrate history on the whole does not show any obvious direction. For instance, mammal evolution does *not* seem to have led inescapably toward humans, and does not show any consistent discernable trend (except possibly toward increased body size). Many lineages do show some sort of trend over time, but those trends were usually linked to available ecological niches, not to an inherent "evolutionary path", and the "trends" often reversed themselves when the environment or the competition changed.

   Models 1, 2, and 3 are all consistent with the known fossil record.
4. Standard "young-earth" creationism

   Creation of separate "kinds" in the order listed in Genesis, in six days, followed by a cataclysmic flood.

   The Flood model is completely falsified, since the fossils appear in a different order than can be explained by any conceivable "sorting" model. Note that this is true not just for terrestrial vertebrates, but also for aquatic vertebrates, pollen, coral reefs, rooted trees, and small invertebrates. For example, ichthyosaurs and porpoises are never (not once!) found in the same layers; crabs and trilobites are never found in the same layers; small pterosaurs and equal-sized modern birds and bats are never found in the same layers. In addition, countless geological formations seem to be the result of eons of gradual accumulation of undisturbed sediment, such as multi-layer river channels and deep-sea sediments, and there are no indications of a single worldwide flood. In addition, the Flood Model cannot account for the obvious sorting by subtle anatomical details (easily explained by evolutionary models), or for the phenomenon that lower layers of lava have older radiometric dates. These are only a few of the problems with the Flood Model. See the flood FAQ for further information.

Creation in six "metaphorical" days is also falsified, since the animals appeared in a different order than that listed in Genesis, and over hundreds of millions of years rather than six days.

5. "Separately created kinds", but with an old Earth.

   Literal creationism won't fly, but could the concept of "separately created kinds" still be viable, with the creations occurring over millions of years? This would require the following convoluted adjustments:

   First, if every "kind", (species, genus, family, whatever) was separately created, there must have been innumerable successive and often simultaneous waves of creation, occurring across several hundred million years, including thousands of creations of now- extinct groups.

   Second, these thousands of "kinds" were created in a strictly correlated chronological/morphological sequence, in a nested hierarchy. That is, virtually no "kind" was created until a similar "kind" already existed. For instance, for the reptile-to-mammal transition, God must have created at least 30 genera in nearly perfect morphological order, with the most reptilian first and the most mammalian last, and with only relatively slight morphological differences separating each successive genus. Similarly, God created legged whales *before* he created legless whales, and *Archeopteryx before* creating modern birds. He created small five-toed horse- like creatures before creating medium-sized three-toed horses, which in turn were created before larger one-toed horses. And so on. This very striking chronological/morphological sequence, easily explained by models 1, 2, and 3, is quite puzzling in this model.

   Third, God did not create these kinds in a sequence that obviously progressed in any direction, as discussed briefly under model 3. This is not necessarily a fatal flaw (mysterious are the ways of God, right?), but it is another puzzle, another unexplained aspect of the fossil record.

   Fourth, what about those species-to-species transitions? They appear to show that at least *some* species, genera, and families arose by evolution (not necessarily all, but at least some.) How can a creationist model be reconciled with this evidence?

   1. "Minor" evolution allowed.

      In this model, the species-species transitions DO represent evolution, but of a minor and unimportant variety. Note, however, that during these bursts of "minor evolution", the evolution took place in an apparently non-directed manner, sometimes crossed genus and family lines, and resulted in just the same sorts of morphological differences that are seen between the other, presumably created, groups of animals.

   2. Separately created fossils.

      In this model, the "species-species transitions" do *not* represent evolution. This implies that *every individual fossil* in the species-to-species transitions must have been separately created, either by creation of the animal that later died and was fossilized, or by creation of a fossil in situ in the rock. I have heard this model called the "Lying God Theory".

In summary, models 1, 2, and 3 (slightly different versions of basic evolutionary theory) are consistent with the fossil record, and go further to *explain* its notable features with a coherent overarching framework. Evolutionary theory has made successful predictions about fossils that were discovered later (e.g. the whale fossils), about genetic patterns, and about numerous other aspects of biology such as the development of disease resistance. Model 4 (literal young-earth creationism) appears unsalvagable, as all of its predictions are wrong. Model 5 (nonliteral creationism, with separately created kinds on an old earth) can just barely be modified to be consistent with the fossil record, but only with bizarre and convoluted tinkering, and only, apparently, if God created the world to make it *look* like evolution happened. In my humble opinion, this still utterly fails to *explain* the record's notable features or to make any useful or testable predictions. It also raises the disturbing question of why God would go to such lengths to set up the appearance of evolution, right down to inserting the correct ratios of radioisotopes in the rocks.

Okay, having blathered on about that, now I'll quit pontificating and get to the main point.

The Main Point

Creationists often state categorically that "there are no transitional fossils". As this FAQ shows, this is simply not true. That is the main point of this FAQ. There are abundant transitional fossils of both the "chain of genera" type and the "species-to-species transition" type. There are documented speciations that cross genus lines and family lines. The *interpretation* of that fact I leave up to you. I have outlined five possible models above, and have explained why I think some of them are better than others. You might disagree with my conclusions, and you can choose the one you think is best, (or even develop another one). But you cannot simply say that there are no transitional fossils, because there are.

As Gould said (1994): "The supposed lack of intermediary forms in the fossil record remains the fundamental canard of current antievolutionists. Such transitional forms are scarce, to be sure, and for two sets of reasons - geological (the gappiness of the fossil record) and biological (the episodic nature of evolutionary change, including patterns of punctuated equilibrium and transition within small populations of limited geological extenet). But paleontologists have discovered several superb examples of intermediary forms and sequences, more than enough to convince any fair-minded skeptic about the reality of life's physical geneology."

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Discover, February 1995, p. 22 "Wabbit or Wodent?" Brief description, with photo, of a probably rodent/lagomorph ancestor.

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